FOREST Science

A QUARTERLY JOURNAL OF RESEARCH AND TECHNICAL PROGRESS

Volume 4 - Number 1 - March 1958

PUBLISHED BY SOCIETY OF AMERICAN FOREST

WASHINGTON, D

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Subscription price is $6.00 per year for complete volumes (one per calendar year), and $2.00 for single number. Add $0.25 for postage to Canadian addresses and $0.50 for postage to other foreign addresses.

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FOREST *Science*

A Quarterly Journal of Research and Technical Progress

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Volume 4
March 1958
Number 1

Forest Soil-Moisture Relations in the Coastal Plain Sands of Southern New Jersey

BY
HOWARD W. LULL
JOHN H. AXLEY

FOREST COVER uses up soil moisture; this affects the amount of precipitation that can go into ground-water storage and into streamflow; and this, in turn, influences the amount of water that is available for domestic, industrial, and agricultural uses. And so it is important in watershed management to determine how different kinds of forest cover utilize the soil moisture, and how they affect the recharging of ground-water storage.

The authors studied some aspects of this problem in the upland part of the New Jersey Pine Barrens, the last major undeveloped source of water in that State. Ground water in this region is held in a reservoir of deep coastal plain sands that can yield substantially more than a billion gallons of water daily for an indefinite period (Barksdale, 1952).

Most of the Pine Barrens' 1,300,000 acres are forested. The upland area, which constitutes about one-half of the Barrens, is covered chiefly with pitch pine (*Pinus rigida* Mill.), shortleaf pine (*Pinus echinata* Mill.), and various oaks including chestnut oak (*Quercus prinus* L.), white oak (*Quercus alba* L.), scarlet oak (*Quercus coccinea* Muenchh.), and black oak (*Quercus velutina* Lam.). Ground cover is commonly a mixture of blueberry (*Vaccinium* spp.) and huckleberry (*Gaylussacia* spp.). How much water is used by the various kinds of cover—oaks compared to pines, for instance, or pine saplings compared to pine poles—is not known.

This question has acquired additional pertinence through the development of practical methods for converting stands of worthless oaks to valuable pitch and shortleaf pine (Little and Moore, 1950). Success of these methods, which involve prescribed burning, is encouraging conversion of considerable areas to pine (Cranmer, 1955). How this change in forest cover affects water supplies has been considered sufficiently important by Rutgers University and the U. S. Geological Survey to warrant an intensive study in which streamflow and ground-water measurements from a prescribe-burned watershed and an unburned watershed will be compared (Buell, 1955).

Previous Investigations

Only a few scattered soil-moisture studies have been conducted to determine water use by woody vegetation. They are valuable for the techniques they describe, and

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for the insights they give on moisture use, particularly as it is affected by depth.

A. H. Hendrickson (1942) first proposed determining water use by forest vegetation through soil-moisture studies. One study of this kind was made by Rowe and Colman (1951) in woodland-chaparral and ponderosa pine in California. Soil-moisture samples to bedrock (3 to 6 feet) were taken weekly during the rainy season, every 2 weeks during late summer and fall, and within 72 hours after storm periods. Annual evapo-transpiration was calculated by summing moisture losses between storms; moisture contents immediately after and before storms were estimated by extrapolating trends developed from sampling.

In a more recent study by Hendrickson and Veihmeyer (1955) water consumption by 10-year-old almond trees was determined from periodic soil-moisture samples taken from April to September by 1-foot increments to a depth of 12 feet; the top 6 feet were sampled every 2 weeks and the lower 6 feet every 4 weeks. Low moisture losses below 9 feet indicated that tree roots had not thoroughly permeated that depth.

Differences in water use by different types of vegetation have been ascribed to the depths to which soil moisture is removed. For instance, Croft (1950) reported from a study in Utah that because of differential root penetrations, at the end of the growing season a soil-moisture deficit of 11 inches was found under aspen, a deficit of 8 inches under adjacent herbaceous cover where aspen had been cut, and a deficit of 3 inches on a site bare of vegetation. According to Hoover (1952) loblolly pine in the Piedmont of South Carolina removed moisture to a depth of 6 feet whereas broom sedge (*Andropogon virginicus*), with shallower roots, dried soil to a depth of 3 feet.

For oak stands in southeastern Ohio, Gaiser (1952) reported that cumulative soil moisture losses during the growing season from a soil 48 inches deep amounted to 23 inches, whereas on two sites with soil depths of 36 inches, losses were 13 and 12 inches. Soil moisture samples were taken weekly by horizons to a maximum depth of 40 inches.

Reduction in rate and amount of moisture removed with increase in soil depth has been reported from moisture measurements made in an orange grove on sandy loam (Pillsbury, Compton, and Picker, 1944), in a pear orchard on heavy clay (Aldrich, Work, and Lewis, 1935), and in loblolly pine and hardwood stands on silt loam (Zahner, 1955).

Hoover, Olson, and Greene (1953) reported rapid rates of loss to a depth of 5½ feet in a loblolly pine plantation on sandy loam, noting that water was withdrawn from the zone in which it was most readily available, regardless of depth. In a 15-year-old loblolly pine plantation and a white oak stand in southern Illinois, Boggess (1953) found almost simultaneous exhaustion of moisture at five depths in the upper 2 feet of soil. Gaiser (1952) also observed that all horizons of the profile simultaneously approached the permanent wilting percentage.

Two studies conducted in the New Jersey Pine Barrens are pertinent to this study. Cantlon (1951) found little difference in soil-moisture contents of annually burned and unburned stands at the 20- and 70-cm. depths; measurements were taken twice weekly between June 15 and August 15. In a root study by McQuilkin (1935) 8- to 9-year-old pitch pine seedlings were found to have taproots reaching depths of 1.5 to 2.5 feet, sapling taproots penetrated 3 to 4 feet, and mature trees had taproots 8 to 9 feet long. These depths probably mark limits of moisture removal (Conrad and Veihmeyer, 1929; Richards and Wadleigh, 1952).

As far as is known, there have been only two studies that have given standard deviations from soil-moisture sampling. Slater and Bryant (1946) reported variation in two soils at Beltsville, Md. Soil

samples, representative of a 4-inch intercept centered at the 6-inch soil depth, were taken in duplicate from 10-foot-square plots about 20 times a season. Standard deviations of moisture contents within plots were 0.75 percent by weight in Beltsville silt loam and 0.53 percent in Muirkirk sand.

Lull and Reinhart (1955) found standard deviations of 1.1 to 5.8 percent for weekly samples from the 0- to 6- and 6- to 12-inch depths taken in sampling plots in the South, West, and Lake States. Sixty-seven percent of the variation occurred within 25-foot-square plots, 20 percent between plots within 100-foot-square blocks, and the remainder, 13 percent, between blocks.

The Present Study

The scope of the study described in this report was limited to the following:

1. *Upland sites* where, for most soil-moisture sampling plots, the water table did not affect the moisture content of the upper 5 feet of soil.
2. *Four kinds of cover:* oaks, shortleaf pine poles, pine saplings, pine seedlings-oak sprouts (reproduction); and a bare area.
3. *Deep, sandy soils* with varying amounts of gravel.
4. *Weekly soil-moisture measurements* in each kind of cover and the bare area during one growing season, mid-April to the last of November.
5. *Soil-moisture measurements* to a depth of 5 feet with occasional sampling to a depth of 12 feet.

Because few soil-moisture studies of this kind have been made, attention was also directed to one of the least understood aspects: soil-moisture variation under forest stands.

Study Area

The study area was in the Lebanon State Forest, about 30 miles due east of the northern section of Philadelphia, Pa., and 20 miles, direct distance, from the Atlantic seacoast. The forest lies a few miles eastward of New Lisbon, N. J. Three soil-moisture sampling plots were located for each of the four kinds of vegetation and the bare area within a square-mile area. Each plot measured 42 feet square (about 1/25th acre), sufficient to permit a 6x6-foot sampling grid of 64 points. The general topography of the area was flat; plots ranged in elevation from about 90 to 110 feet above sea level.

Vegetation. The pine-pole plots were characterized by an overstory of eight to twelve 100-year-old shortleaf pine poles about 55 feet tall and averaging 9 to 10 inches d.b.h., overtopping 24 to 31 chestnut, black, and white oaks 2 to 3 inches in diameter and about 35 feet tall. Ground cover consisted of 800 to 1,000 stems of blueberry and huckleberry.

The overstory of the oak plots was composed of 25 to 27 stems of scarlet and black oaks about 32 years old. Average diameter was about 4 inches and average height varied from 40 to 57 feet. Huckleberry and blueberry made up the ground cover with fairly extensive patches of moss covering some areas.

Pine saplings, about 15 years old, grew in thickets of 110, 58, and 118 stems in plots 1, 2, and 3 respectively; average diameters were 2.5, 3.3, and 3.0 inches and height averaged about 18 feet. The blueberry ground cover had about the same density as that of the hardwood plots.

Reproduction plots contained a fairly thick stand of shortleaf pine, averaging 6 feet in height, and 33 to 40 scattered clumps of oak sprouts covering 16 to 22 percent of the plot areas. Seedlings and sprouts were 7 years old. Ground cover consisted of blueberry and huckleberry stems, sweetfern (*Comptonia* spp.) and sedge (*Carex* spp.)

On the bare plots, a heavy concentration of herbicide[1] was applied to the herbaceous ground cover on April 19, 2 weeks after the beginning of sampling. By the last of June, leaves of the vegetation had

[1]The herbicide "Telvar" (CMU), was applied at the rate of 80 pounds per acre.

turned brown and almost all the vegetation was killed by mid-July.

Soils. Four soil types were identified: Evesboro sand at 10 plots, Evesboro fine sand at one plot, Lakewood sand at two plots (one pine pole and one pine sapling), and Lakehurst sand at two plots (bare).

Evesboro is a gray-brown podsolic soil whereas the Lakewood and Lakehurst series are podsols. The Evesboro soil is well drained and not so deeply leached as the podsols. The Lakewood and Lakehurst soils are members of the Lakewood catena, in which Lakewood occupies the better-drained position. These soils are considered to be among the poorest in the United States for agricultural purposes (U. S. Dept. Agric., 1938).

Excepting on the bare plots, which had no accumulation of surface organic materials, litter averaged about 1 inch deep. Humus extended into the mineral soil 0.5 to 3.0 inches. The texture of the 0- to 5-foot soil depth averaged 24 percent gravel, 71 percent sand, and 5 percent finer materials. Coarse materials persisted to a depth of at least 12 feet. Gravel tended to increase with depth: it averaged 8 percent in the surface foot, 16 percent in the second foot, and about 30 percent (gravelly sand) in the next 3 feet. The average bulk density for all plots was 1.60. Bulk density increased with depth, ranging from an average of 1.41 for the first foot to 1.78 for the fifth foot.

For the forested plots the average maximum moisture content per foot of soil depth for the period of record was 1.44 inches and the minimum value was 0.33 inch. With an average bulk density of 1.60, these are equivalent to 7.5 percent and 1.7 percent by weight, values very similar to the field capacity and wilting percentage of Norfolk sand reported by Peele and Beale (1950), namely 7.1 percent and 2.1 percent.

Weather. Rainfall for the period was 16 percent below normal; August was wettest because of hurricane rains. In May, July, August, and October, air temperature averaged 2° to 3° F. above normal; June was 4° and September 3° below normal. For New Jersey, July was the hottest and driest month since 1885 and August the sixth hottest and wettest month (U. S. Dep. Comm., 1955).

Methods

At each of the fifteen plots six soil-moisture samples were taken weekly. Samples were taken with a soil-sampling tube, at a randomly located point, from 0- to 6-inch and 6- to 12-inch depths and from 1- to 2-foot, 2- to 3-foot, 3- to 4-foot, and 4- to 5-foot depths. (In analysis, moisture contents of the upper two depths were combined into a single value for the 0- to 1-foot depth.)

Samples were weighed on a Toledo scale to the nearest 0.1 gram, ovendried for 24 hours at 105° C., and reweighed. They were then sieved through a 20-mesh sieve, and the fine gravel was weighed. In the course of 33 weekly samplings during the 7-month sampling period, about 3,000 samples were taken.

As time permitted, samples were taken below 5 feet to a maximum depth of 12 feet, using an extension tube. Deep samples were first taken from selected plots in July, then twice in August, once in September, twice in October, and twice in November. In all, more than 300 samples were taken below 5 feet.

Sampling for soil-moisture variation analysis was fitted into field work as time permitted. Variation samples were taken on four occasions: April 29 to May 6, May 20 to 27, June 17 to 24, and October 7 to 14. On each occasion four points were randomly located on each of one or more soil-moisture plots in each cover type; 6 samples were taken at each point, a total of 24, from depths sampled periodically.

For more intensive sampling, one supplemental sampling plot, 12x12 feet in size, was laid out in each type adjacent to one of the soil-moisture plots. Soil-moisture samples were taken from the same six depths at

points on a 3x3-foot grid system, a total of 25 points and 150 samples per plot. Each plot was sampled only once.

In all, 1,300 variation moisture samples were taken and treated the same way as the periodic samples: weighing, drying, reweighing, sieving, and weighing.

Bulk density samples were taken with a small San Dimas sampler with a soil core volume of 71 cm.^{3}; the cylinder was 2 inches high and had an inside diameter of 1⅜ inches (Broadfoot, 1954). Samples were taken from each successive 6-inch depth to a depth of 5 feet; 90 samples were taken at each plot. Gravel content of each sample was determined.

Soil-moisture content in inches of water was calculated for each soil-moisture sample from the equation:

$$\text{Inches of water} = \frac{\text{moisture percent}}{100} \times \text{bulk density} \times \text{inches soil depth.}$$

Bulk densities used in the above equation are expressed in grams per cubic centimeter. These were estimated for each sample from its gravel content, using bulk density-gravel content linear regressions developed for this purpose for each plot. In these equations the "a" constant varied from 1.33 to 1.53, and the "b" coefficient ranged from $0.00423X$ to $0.00803X$ where X = percent gravel content; correlation coefficients "r" ranged from 0.47 to 0.95 with coefficients for 9 of the 15 plots 0.80 and greater.

A standard rainfall can was placed in an opening adjacent to each of five plots selected to give a well-distributed measurement of rainfall over the experimental area. Daily measurements were taken at one can and weekly readings at four. A hygrothermograph was operated at the Coastal-Oak-Pine Research Center of the Forest Service.

Results

Comparison of Soil-Moisture Regimens

Soil moisture contents of the 0- to 5-foot depth at each sampling are shown in Figure 1 together with rainfall. At the beginning and ending of the record, moisture contents were about the same: an average of 5.83 inches on April 14 and 5.39 inches on November 25. Between these dates were three periods of wetting—with peak moisture contents on April 29, August 19, and October 28—and three major periods of drying: April 29 to May 27, June 14 to July 29, and August 19 to September 9.

Two major relationships are apparent. First, soil-moisture regimens are very similar for the five kinds of cover. They tended to dry together and wet together. Relative coincidence in the three peak periods and the periods of depletion are striking. No one cover differed consistently from the others.

Second, within these similar trends was considerable range in moisture-content variation—large differences on certain dates and much less on others. For the six periodic samplings from June 3 to July 1, for instance, ranges between maximum and minimum moisture contents of the five cover types were 0.59, 1.19, 0.96, 1.20, 0.83, and 1.41 inches. Also, relative positions were variable; no single type was consistently wettest at the three peak moisture contents or consistently driest at the end of the three drying periods.

Differences between cover. To determine whether the variation within trends was significant, analyses of variance of data from 11 different samplings were computed. Key sampling dates (Fig. 1) included dates of beginning and end of record, dates of moisture peaks and lows, and—for later comparisons of variation—dates of variation sampling. For each date, degrees of freedom were as follows:

	D.f.
Cover	4
Depth	4
Cover × depth	16
Error	50
Total	74

Mean squares are given in Table 1.

TABLE 1. Soil moisture content, in inches, on 11 sampling dates, and associated mean square variances.

Date	Mean moisture content under—					Source of Variation			
	Pine poles	Oaks	Reproduction	Pine saplings	Bare soil	Cover	Depth	Cover × depth	Error
Apr. 14	6.30(1)[1]	6.27(2)	5.83(3)	5.59(4)	5.16(5)	0.07	0.77**	0.05	0.06
Apr. 29	6.71(1)	6.02(3)	6.45(2)	6.59(4)	5.47(5)	.11*	1.24**	.09	.04
May 20	3.66(3)	3.93(1)	3.89(2)	3.00(4)	2.95(5)	.05	.09	.06	.06
June 24	3.61(4)	3.60(5)	4.43(1)	4.01(2)	3.85(3)	.06	.06	.02	.04
July 29	2.05(2)	1.78(4)	1.91(3)	1.35(5)	2.82(1)	.15**	.09*	.04	.03
Aug. 5	1.89(4)	1.61(5)	2.30(2)	2.10(3)	2.54(1)	.07	.02	.02	.03
Aug. 19	5.88(3)	5.80(4)	6.46(2)	6.57(1)	5.25(5)	.17	.81**	.06	.07
Sept. 15	3.41(1)	2.70(5)	2.88(4)	3.02(3)	3.34(2)	.05	.03	.02	.04
Oct. 14	4.04(4)	3.78(5)	4.72(1)	4.12(3)	4.70(2)	.09*	.93**	.09**	.03
Oct. 28	6.22(5)	6.76(3)	7.17(1)	6.92(2)	6.62(4)	.07	.42	.12	.17
Nov. 25	5.85(1)	5.08(5)	5.23(4)	5.41(2)	5.36(3)	.05	.54**	.02	.04

[1]Numbers in parentheses indicate ranking in order of wetness.
**Significant at 1% level.
*Significant at 5% level.

In the 11 samplings, differences between cover were statistically significant three times: at the 5-percent level on April 29 and October 14 and at the 1-percent level on July 29. These did not establish consistent differences. The significance difference for the peak April 29 date, for instance, did not occur at later peak dates; the July 29 significant difference was followed a week later with differences that were not significant. Likewise, little importance can be attached to the October 14 significant difference because the relative positions of almost all kinds of cover changed in preceding and subsequent samplings. From this analysis, no real difference in moisture regimen was indicated.

For the forested plots, the uniformity in soil-moisture utilization indicates that the soil depth considered, 0 to 5 feet, was well occupied by the roots of each type.

By the last of June the vegetation in the bare site was brown, transpiration ceased, and moisture losses thereafter were dependent on evaporation alone, a process which by its action—working from the soil surface downward—does not remove water so rapidly as evapo-transpiration. Hence there was a tendency for higher moisture contents to prevail at the bare plot.

Differences between depths. Moisture-content differences between 1-foot depths proved significant 6 of the 11 times. Five of these, all highly significant, occurred during the six wet or moderately wet dates analyzed. One, significant at the 5-percent level, occurred on one of the five dry dates. Depth differences were not significant for the October 28 peak values of record. Thus, as would be expected, differences between depths were not significant when the soil approached either a uniformly dry or wet condition.

The cover × depth interaction was significant at the 1-percent level on October 14, when sampling showed that the bare and reproduction plots were wetter in the 2- to 5-foot depths than the other types. Otherwise, variation with depth was consistent for all types.

Maximum and minimum moisture contents. Maximum and minimum moisture contents, given in Table 2, are based on averaging values for the three wettest dates—April 29, August 19, and October 28—and the two driest—July 29 and August 5. Under wet conditions there was a marked decrease in moisture content with depth, whereas minimum values varied but little. This

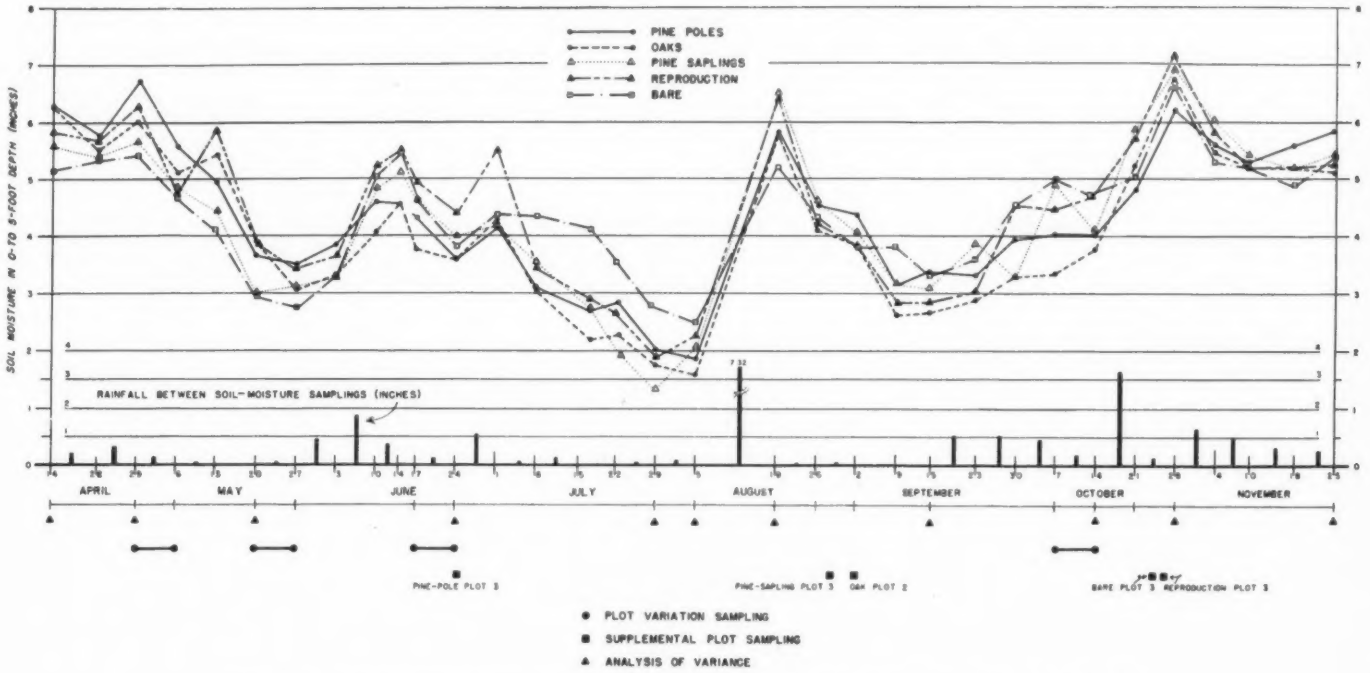

FIGURE 1. *Soil-moisture record at the 0- to 5-foot depth for each vegetative cover and the bare area; rainfall record and dates of soil-moisture vegetation sampling and analysis.*

agrees with results of the foregoing analysis.

Values given in Table 2 were subjected to an analysis of variance. For maximum moisture contents, differences between types were not significant ($F = 0.86$), and differences between depths were highly significant ($F = 11.12$). For minimum values, differences between types were significant ($F = 4.76$), and differences between depths were not significant ($F = 2.38$).

The highly significant difference in maximum moisture contents between depths is due largely to higher moisture contents for the upper 2 feet of soil (Table 2). This, in turn, is closely related to their lesser gravel content: average gravel content of the first and second foot of soil was 8 and 16 percent; and for the next 3 feet in turn, 29, 33, and 33 percent.

The significant difference between types for minimum values can be ascribed largely to the greater moisture content of the bare area in late July and early August. The least significant difference was 0.15 inch; differences in mean minimum moisture between the bare plots and pine, oak, sapling, and reproduction plots were 0.14, 0.18, 0.22, and 0.11 inch, respectively.

Evapo-Transpiration

When no percolation occurred to depths below 5 feet, weekly evapo-transpiration was calculated by one of two methods, depending on whether measurements showed soil-moisture depletion or accretion.

When soil moisture was depleted, evapo-transpiration was considered equal to the amount of depletion plus the amount of rainfall. For example, average moisture contents of the pine-pole plots were 6.30 inches on April 14 and 5.78 inches on April 22, a depletion of 0.52 inch. Rainfall of 0.39 inch that occurred during that interval was assumed to have evaporated and transpired, giving a total evapo-transpiration of 0.91 inch for the week.

If, during the week, accretion rather than depletion occurred, evapo-transpiration was considered as the difference between rainfall and accretion. For example, moisture contents of the pine-pole plots on May 27 and June 3 were 3.51 and 3.86 inches, respectively, an accretion of 0.35 inch. Dur-

TABLE 2. Maximum and minimum soil-moisture contents, in inches, by 1-foot depths for each cover.

Depth (feet)	Pine poles	Oaks	Pine saplings	Reproduction	Bare
		MAXIMUM VALUES			
1	2.02	1.75	1.98	1.91	1.58
2	1.57	1.37	1.41	1.67	1.14
3	1.21	1.24	1.42	1.37	1.21
4	1.06	1.32	1.15	1.50	1.37
5	1.18	1.17	1.41	1.07	1.39
Total	7.04	6.85	7.37	7.52	6.69
		MINIMUM VALUES			
1	.22	.32	.20	.28	.26
2	.37	.32	.35	.46	.37
3	.38	.33	.24	.40	.66
4	.44	.32	.24	.30	.57
5	.33	.26	.32	.47	.59
Total	1.74	1.55	1.35	1.91	2.45

ing this period, there was 0.96 inch of rainfall; as 0.35 inch accreted to the soil, the remainder, 0.61 inch, was considered evapo-transpiration.

Evapo-transpiration was estimated for three periods when percolation below 5 feet occurred: August 5 to 19, October 14 to 21, and October 28 to November 4. Each was a period of heavy precipitation when rainfall exceeded storage opportunity; as an unknown amount of moisture moved below 5 feet, weekly evapo-transpiration for the upper 5 feet could not be calculated. For these periods, weekly values were estimated by extrapolating the trend of the mass curves (Fig. 2) one week ahead.

Total evapo-transpiration from the 0- to 5-foot depth for the period of record was as follows:

	Moisture (inches)
Pine poles	20.84
Oaks	22.07
Pine saplings	22.49
Reproduction	23.19
Bare	17.24

From an analysis of variance of the weekly evapo-transpiration values, differences between cover types were not significant ($F = 1.33$). But as expected, differences between weekly values were highly significant ($F = 6.76$), reflecting the influence on evapo-transpiration of weekly variation in rainfall, soil-moisture content, and seasonal variation in air temperature. Thus, even though differences between cover types were as great as 5.95

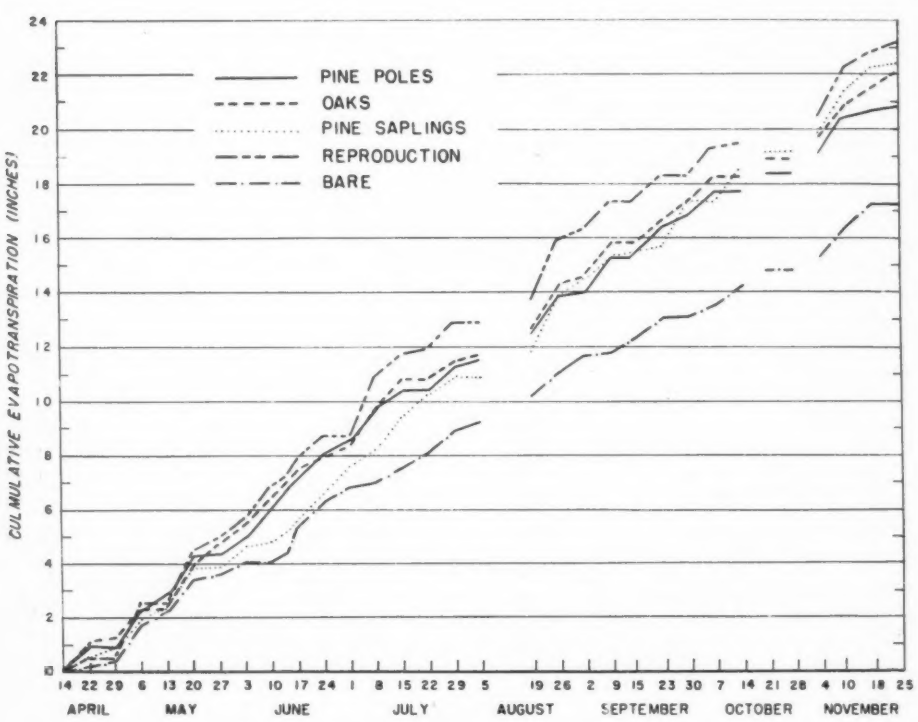

FIGURE 2. *Cumulative evapo-transpiration for each kind of cover during period of record.*

inches, they indicated only a chance difference when evaluated in respect to the large variation stemming from inconsistent interaction of conditions with dates.

However, inconsistencies in individual weekly values of evapo-transpiration tend to iron out with continued sampling, as shown for example in the following values for the oak and pine sapling plots:

Period	*Oaks*	*Pine saplings*
June 14-17	0.80	0.47
June 17-24	.46	.92
June 24-July 1	.40	.93
July 1-8	1.35	.68
Total	3.01	3.00

The tendency to minimize differences as sampling progresses suggests that further consideration be given to the causes of the greatest difference, that between the forested plots and bare plots.

As the soil-moisture records of Figures 1 and 2 show, this difference was due partially to a reduction in soil-moisture depletion in July after applications of a herbicide. A second causative factor is interception. (Evapo-transpiration, as calculated, includes evaporation of precipitation intercepted by the vegetation as well as soil-moisture depletion.) Based on Hoover's (1953) interception study in loblolly pine, a net interception of 10 percent may be a reasonable value for interception of the rainfalls experienced. If so, forest vegetation would have intercepted and evaporated 2.43 inches of rainfall, which accounts for about one-half of the 5-inch difference in evapotranspiration between the bare plots and the forested plots.

Average daily soil-moisture depletion for the three major drying periods are given in Table 3. Rates ranged from 0.05 to 0.13 inch with averages for the five types ranging from 0.07 to 0.09 inch per day.

To test significance of differences between drying rates of the cover and three periods, an analysis of variance was made, using variance of the three replicate plots for the error source. Cover and the interaction between cover and periods were not significantly different, whereas differences in rates for the three drying periods were significant at the 1-percent level ($F = 5.88$).

Differences in rates between the May and August–September periods may be attributed to the season. During most of May, deciduous vegetation was not in full leaf and daily mean temperatures averaged 67°F. In late summer, the canopy was in full leaf and temperatures averaged 4°F. higher. Drying periods encompassed similar ranges of moisture content.

During the July–August period, mean daily temperature was 79°F.—12° and 8° higher, respectively, than the earlier and later drying periods. Despite this, the midsummer rates of moisture loss were in most instances slower. However, moisture content at the beginning of the July–August period was not so high as those of the other two periods, and soils were much drier at

TABLE 3. Mean daily soil-moisture depletion rates for three periods, for each cover, in inches.

Cover	May 6–27	July 1–Aug. 5	Aug. 19–Sept. 15	Mean
Pine poles	0.094	0.063	0.088	0.082
Oaks	.094	.075	.111	.093
Pine saplings	.079	.058	.122	.086
Reproduction	.060	.091	.128	.093
Bare	.087	.052	.068	.069
Mean	.083	.068	.103	.085

the end of the period. Thus the soil was generally drier; and, as rate of loss is positively correlated with moisture content, lower rates in July–August could be expected.

Accretion and Depletion by Foot-Depths

The soil-moisture record by foot-depths for each kind of cover is given in Figure 3. Several moisture-accretion and -depletion relationships for the forested sites are apparent: (1) Depletion is concurrent at almost all depths in the first few weeks of record, and there appears to be no tendency for lower depths to dry subsequent to upper depths; (2) after drying of the spring-wet soils, ordinary summer rainfalls wet primarily only the upper 2 feet of soil; (3) immediately after summer wetting, the upper 2 feet of soil, which has higher moisture content, tends to dry more rapidly than the lower 3 feet; after a week to 10 days, drying rates are about the same for all five 1-foot depths; (4) at minimum moisture contents the upper 5 feet of soil is uniformly dry, as evidenced by the August 5 and September 15 measurements; and (5) because of lower water-holding capacity and lesser wetting from summer rainfall, moisture contents of the lower 3 feet fluctuate much less than those of the top 2 feet.

The effect that poisoning of vegetation has on bare-plot drying was evident after June 24: the upper 2 feet of soil dried much more rapidly thereafter than the lower 3 feet subject to less evaporation because of the insulating effect of the overlying soil.

To compare accretion and depletion by depths, weekly values were computed and summed for the period of record. Results are given in Table 4. Since moisture contents at the beginning and ending of the period were similar, total depletion values tend to be balanced by total accretion.

Thirty percent of the moisture removed from the upper 5 feet of soil came from the upper foot, 22 percent from the second foot, and 16 percent came from each of the next 3 feet. These correspond roughly to findings of others. Aldrich, Work, and Lewis (1935) report 34, 28, 22, and 16 percent moisture extracted from successive foot-depths by pear trees from the upper 4 feet of soil. A similar study under mature orange trees growing in sandy loam

TABLE 4. Soil moisture accretion and depletion by 1-foot soil depths for each kind of cover, in inches.

Depth (feet)	Pine poles	Oaks	Pine saplings	Reproduction	Bare	Mean	Percent of total
			ACCRETION				
1	4.11	4.07	4.86	4.82	3.87	4.35	29
2	3.15	3.26	3.43	3.66	3.04	3.31	22
3	2.34	2.27	2.57	3.02	2.00	2.44	16
4	1.50	2.05	2.63	3.36	2.94	2.50	17
5	2.35	2.25	2.16	2.22	2.88	2.37	16
Total	13.45	13.90	15.65	17.08	14.73	.....	....
			DEPLETION				
1	4.45	4.30	5.07	5.14	3.93	4.58	30
2	3.11	3.39	3.04	3.85	3.09	3.30	22
3	2.04	3.00	2.50	2.90	1.87	2.46	16
4	1.62	2.27	2.65	3.19	2.82	2.51	16
5	2.52	2.54	2.32	2.12	2.52	2.40	16
Total	13.74	15.50	15.58	17.20	14.23	15.25	....

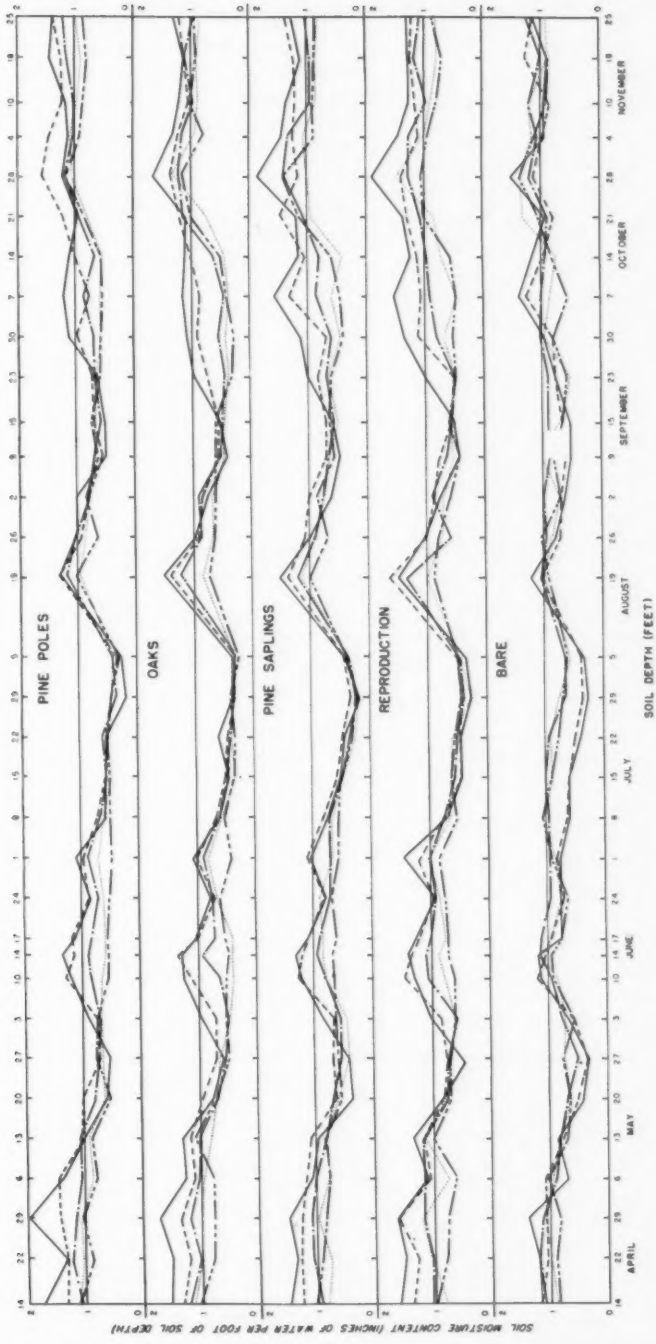

FIGURE 3. *Soil-moisture record by one-foot depths for each kind of cover.*

gave values of 37, 30, 15, 11, 4, and 3 percent for the upper 6 feet of soil (Pillsbury, Compton, and Picker, 1944).

Moisture Losses from Depths Below Five Feet

By the last of May the fifth foot of soil had been drying for a month (Fig. 3), and it can be assumed that moisture was also being extracted from lower depths. Though time and labor did not permit weekly sampling below 5 feet, on ten occasions samples were taken, usually in duplicate, from lower depths to a maximum depth of 12 feet.

Pine poles. On July 8, the 6-, 7-, and 8-foot depths were about as dry as the upper 5 feet, and the 9- and 10-foot levels were somewhat wetter (Fig. 4). By the first of August, the 6- to 10-foot depth probably reached its driest midsummer value. The August 19 sampling revealed that heavy rainfall of the preceding week had recharged the soil. A layer of red clay mixed with sand at the 10-foot depth may have restricted drainage and caused the high moisture contents.

The next three samplings (September 15 and October 4 and 12) indicated continuous drying to about the moisture content reached in early August. On November 1, recharge appeared to be proceeding both from the surface and from a rising water table; and this recharge continued to November 17, when the moisture content

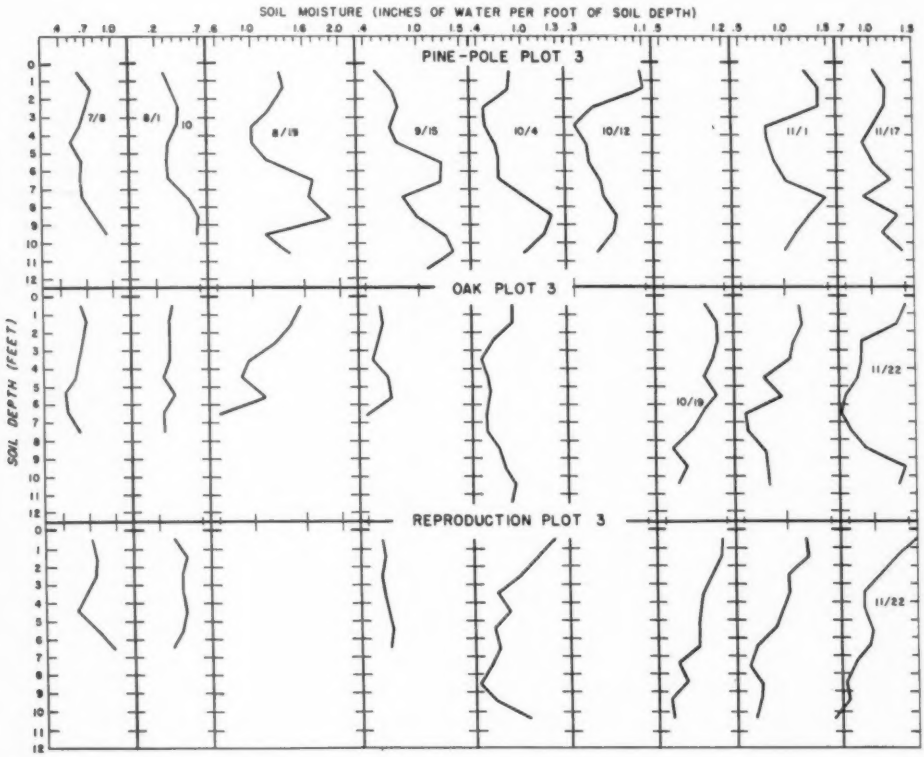

FIGURE 4. *Soil-moisture record for pine poles, oak, and reproduction at the 0- to 12-foot depth.*

of the 6- to 10-foot depth averaged 1.15 inches per foot, probably close to field capacity. Simultaneous recharge from the soil surface and the water table might be explained by a general rising of the water table due to recharge of adjacent swamps by rainfall.

The depth of moisture extraction indicated that pine and oak understory roots extend at least to a depth of 11 feet, 2 feet deeper than the 9-foot taproot of a pitch pine excavated by McQuilkin (1935).

Oaks. A few 5- to 8-foot samples taken before October 4 show trends similar to those in the pine plots. October 4 and November 1 samplings indicated somewhat lower moisture contents than those on the pine plot. Recharge started by November 22 but was not so advanced as for pine poles on November 17. Again, the phenomenon of recharge from above and below is evident.

Average moisture content for the 5- to 11-foot depth on November 22 was 0.93 inch per foot, or an overall difference from the pine plot of 1.32 inches less moisture for the lower 6 feet. If the pine and oak plottings of October 4 and November 1 are compared, moisture does not appear to be extracted so rapidly below 8 feet in pine as in oak. Sampling did not extend deep enough to determine whether oaks or pine poles had the deeper rooting system.

Reproduction. Samplings up to and including October 19 showed moisture contents very similar to those of the oak plot. Moisture depletion below 2 to 3 feet was probably almost entirely due to oak sprouts because, as McQuilkin (1935) reports, the taproots of 8- to 9-year-old pitch pine seedlings (and presumably shortleaf pine) reach depths of 1.5 to 2.5 feet. There was no evidence of recharge from below in November.

Results here indicate that 7-year-old oak sprouts and shortleaf pine seedlings will use as much water as a 32-year-old stand of oak, and perhaps more water than a pine-pole stand. The technique of prescribed burning every 5 years to kill hardwood sprouts may thus be a measure of water conservation, and, incidentally, could encourage growth of the pine by making greater water supplies available.

Pine saplings. On July 8 the sixth foot was depleted to 0.66 inch and the seventh foot was wet—1.67 inches. After the heavy August rainfall, moisture was gradually reduced in the seventh- and eighth-foot depths to 0.48 and 0.81 inch respectively by October 12. The 9-foot depth was wet—2.45 inches. After that, moisture contents below 5 feet increased.

The root depth of 8 feet, indicated by this record, is about twice the depth reported by McQuilkin (1935) for pitch pine saplings. If 8 feet is a representative root-depth for sapling stands, conversion of oak to pine will result in a shorter-rooted tree for at least 15 years and may thereby conserve water supplies. Whatever saving may result could, however, be offset to the extent that winter transpiration of pine exceeds that of oak.

Bare area. On July 8 the moisture content at 5 feet was 0.79 inch and at 6 feet 3.00 inches. By October 4 the 6-foot value had been reduced to 0.65 while the 7-foot moisture was 1.11 inches. After that, moisture contents increased.

The bare area would thus require the least amount of rainfall for fall recharge. For watershed-management purposes of conserving or increasing water supplies, this finding is academic as long as considerable and continuous effort is required to keep vegetation from occupying an area.

Total moisture depletion. Though scanty, the above data, particularly for the pine poles, give some basis for estimating moisture consumption from depths below 5 feet. Evapo-transpiration at these depths was apparently divided into two periods; from the beginning of the spring depletion to the August recharge and from the August recharge to the minimum reached on October 12. After that, depletion was masked by recharge.

Using the November 17 values as estimated field capacities (the August 19 maxima probably resulted from restricted drainage) and the August 1-10 and October 12 values as minima, depletions were calculated as shown in Table 5. About 5.37 inches of water was depleted from the 5- to 10-foot depth, a little more than one-fourth of the 20.84 inches previously estimated to have been depleted from the upper 5 feet. Thus total evapo-transpiration was about 26.21 inches for the 7-month period.

This estimate is high in comparison with Kittredge's (1938) estimate of 20 to 30 inches of annual water loss for this region, based on subtracting runoff from rainfall. On the other hand, the 5 months not accounted for are months of low water loss; evapo-transpirometer records from Seabrook, N. J., show that losses from November through March are 22 percent of those from April through October (Mather, 1954). Applying this percentage gives a winter estimate of 5.76 inches, which—added to the growing season total—gives an annual value of 31.97 inches. This estimate still does not include moisture losses below 10 feet, but it is doubtful if additional losses would amount to much more than 1 inch—based on the reduction in loss between the first and second 5-foot depths and McQuilkin's (1935) report that the taproot does not penetrate much more than 9 feet.

One reason for the high estimate of annual evapo-transpiration, as noted previously, may be seepage losses during wet periods to depths below the sampling zone. High losses may also be related to the unusually high summer temperatures. As the soil-moisture records show, depletion was occurring steadily throughout the summer, and moisture supplies were limited only for brief periods. Under these conditions, moisture loss can be related to the amount of solar radiation received, and greater than normal losses could be expected.

Soil-Moisture Variation Between and Within Plots

Soil-moisture variation between replicate plots for each kind of cover was calculated from the mean square errors given in Table 1. The standard deviations given below are for five consecutive 1-foot samples taken at one point; depth variance has been subtracted.

Cover	*Standard deviation, inches per foot*	*Coefficient of variation, percent*
Pine poles	0.21	23
Oaks	.24	28
Pine saplings	.22	25
Reproduction	.21	23
Bare	.32	36

For all types, the coefficient of variation was 31 percent; subtracting depth variance reduced it to 27 percent. As can be ex-

TABLE 5. Soil-moisture depletion below the 5-foot depth at pine-pole plot 3, in inches.

	Soil moisture					
Depth (feet)	Maximum Nov. 17	Minimum Aug. 1-10	Depletion	Minimum Oct. 12	Depletion	Total depletion
6	1.00	0.31	0.69	0.46	0.54	1.23
7	1.22	.34	.88	.61	.61	1.49
8	.90	.54	.36	.63	.27	.63
9	1.30	.66	.64	.76	.54	1.18
10	1.11	.66	.45	.72	.39	.84
Total	———	———	3.02	———	2.35	5.37

pected, subtraction of variance attributable to types did not further reduce the coefficient.

To determine the variation of moisture content within the 42x42-foot plots, 24 soil-moisture samples were taken on each plot on four separate occasions. Standard deviations and coefficients of variation are as follows:

Cover	*Standard deviation, inches per foot*	*Coefficient of variation, percent*
Pine poles	0.16	18
Oaks	.19	20
Pine saplings	.19	22
Reproduction	.19	20
Bare	.23	23

The average within-plot deviation of 0.19 inch is equivalent to 1-percent moisture content by weight. This is close to the values of 0.75 and 0.53 percent reported by Slater and Bryant (1946) for 10x10-foot plots and to the 1- to 2-percent values reported by Lull and Reinhart (1955) for 6x6-foot plots.

Subtracting depth variance reduced the coefficient of variation for total error from an average of 37 percent to 20 percent, variation in depth being greater for the 5 samplings considered in this analysis than for the 11 samplings of between-plot variance.

Standard deviations (excluding depth variation) and coefficients of variation for the five 12x12-foot supplemental plots were as follows:

Cover	*Standard deviation, inches per foot*	*Coefficient of variation, percent*
Pine poles	0.16	21
Oaks	.12	19
Pine saplings	.16	19
Reproduction	.13	14
Bare	.34	31

Despite the fact that sampling in these plots was about 80 times more intense than in within-plot sampling (125 samples in a 144-square-foot plot vs. 20 samples in a 1,764-square-foot plot), the standard deviation and coefficients of variation for the forested plots are not greatly reduced. Summarizing, between-plot coefficients of variation for the forested plots ranged from 23 to 28 percent, for within-plots 18 to 22 percent, and for the supplemental plot 14 to 21 percent. The uniformity of moisture variation and of moisture content stems from the uniformity in climate, soils, and topography of the experimental area. Soils studied were all sands; there was little variation in rainfall over the area; and differences in elevation, slope, and aspect were slight.

Conclusions

1. Soil-moisture measurements during the growing season on upland sites in the New Jersey Pine Barrens indicated that stands of shortleaf pine and oak scrub used about the same amount of water at about the same rate from the upper 5 feet of soil. Both removed moisture to a depth of at least 12 feet, the lowest depth sampled.
2. Evapo-transpiration from 7-year-old pine seedling-oak sprout stands was governed largely by the sprouts, which removed moisture as rapidly and from the same depth as older oak stands.
3. A 15-year-old stand of shortleaf pine saplings utilized moisture to a depth of 8 feet; this was about 4 feet less than depths utilized by the pine-pole and oak stands, indicating withdrawal of a smaller amount of moisture.
4. Soil-moisture was evaporated from the bare area to a depth of 6 feet, the smallest depletion of soil moisture. In respect to water supply, this is of little practical importance because bare areas do not occur naturally in this region.
5. Total evapo-transpiration from the 0- to 5-foot depth for the period of record ranged from 17.24 inches for the bare plot to an average of 22.15 inches for the four forested conditions. Differences were not statistically significant.
6. Based on the soil-moisture record for the 0- to 10-foot depth, evapo-transpiration from a pine-pole plot amounted to 26.21 inches for the 7-month period;

20.84 inches came from the 0- to 5-foot depth.

7. Within the 0- to 5-foot depth, soil-moisture depletion proceeded simultaneously within each foot-depth and tended toward the same rate. During the period of record, 30 percent of moisture removed came from the upper foot, 22 percent from the second foot, and 16 percent from each of the next 3 feet.
8. Generally, standard deviations at any one sampling, of 1-foot samples to a depth of 5 feet, were about one-third of the mean moisture contents and one-fifth to one-fourth when depth variance was subtracted. Variation of 1-foot samples was similar within 12x12 and 42x42-foot plots, and between 42x42-foot plots within a square-mile area.

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Review by H. A. Fowells

Forest Service, U. S. Department of Agriculture

This annotated bibliography is a timely contribution. Widespread interest in the nutrition of forest trees and in the possibilities of fertilizing forests has sent foresters scurrying to card files and indexes for sources of information. With this 303 page bulletin the authors have provided a ready source by bringing together 700 references, many from foreign literature with translated titles. Most references have been abstracted with sufficient detail to give the reader a good summary of the research problem and the results.

The authors have prepared a subject matter index for the more comprehensive studies reported. Complete indexing would have been desirable but the authors felt that they could not undertake it. However, that provided, with 12 subjects including the major nutrients, is certainly helpful to anyone looking for information. For their foresight and effort in compiling this bibliography, the authors and their cooperator, the Nitrogen Division of Allied Chemical and Dye Co., deserve much credit.

Localized Ecotypic Variation in Western White Pine

BY
A. E. SQUILLACE
R. T. BINGHAM

EVIDENCE OF ECOTYPIC or racial variation has been reported for many tree species. In most cases the variation was associated with localities differing greatly in latitude, longitude, or elevation, and covering widely separated portions of the total range of the species concerned. This type of variation has been observed almost universally, especially where the species involved has a wide distribution. Variation occurring within relatively small portions of the total range of a species, however, has received less attention.

This report presents evidences of ecotypic variation in western white pine (*Pinus monticola* Dougl.) occurring within a very small portion of the total range of the species, and discusses application of the findings. The character and extent of the differences, though based mostly upon the early stages of tree growth, suggest that they may be of considerable practical importance.

Literature Survey

A very extensive literature on provenance, racial variation, geographic races, and ecotypes of forest trees has been published during the past 100 years. The average forester is understandably confused by conflicting and overlapping terminology. Either Rudolf's (1955) report on tree races or Wakeley's (1954) brief article is an excellent starting point for the person interested in inherent variation of trees as conditioned by environment. Rudolf uses the terms "race" and "ecotype" interchangeably, pointing out the confusion existing among foresters due to the use of less precisely defined terms as geographic, altitudinal, climatic, and local races. His use of the term ecotype, from Turreson (1925), well described by Daubenmire (1947), is in keeping with the usage preferred by the authors. The term ecotype (genetically distinct race differentiated by climatic, edaphic, biotic, photoperiodic, or other factors of environment peculiar to the locality) is sufficiently broad to include most of the types of "races" mentioned above.

According to Langlet (1936), critical research on ecotypic variation in forest trees began in Europe with the work of de Vilmorin (1862) and progressed rapidly thereafter due to widespread planting fail-

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ures experienced with *Pinus sylvestris* L. and *Picea abies* (L.) Karst. Knowledge of the importance of provenance was greatly increased by the works of Kienitz (1879), Cieslar (1887-1923), and others. This extensive early literature has been summarized by Schott (1904) and several later workers, including Pearson (1914), Eckbo (1916), and Baldwin (1933); hence, it need not be reviewed here. Instead, the more recent American literature concerning ecotypic variation within native species and a few common exotics is covered.

Following the late 19th and early 20th century European efforts, pioneering American studies yielding information on ecotypic variation of *Pinus ponderosa* Laws. (Weidman, 1939) and *Pseudotsuga menziesii* (Mirb.) Franco (Munger and Morris, 1936) were started in the western United States about 1910. The ponderosa pine study proved the existence of ecotypes within the species and indicated that those originating near the north Idaho planting site, or within 200 miles under roughly similar climatic conditions, were best adapted at the planting site. A companion study (Munger, 1947) also delineated ecotypic variation in ponderosa pines from widely separated localities. The equally important early study with Douglas-fir showed that ecotypes existed within that species, and that their reaction to environment varied at 6 planting sites ranging in elevation from 1,100 to 4,600 feet. Twenty years after planting, significantly different altitudinal and geographic ecotypes were apparent.

With the great increase in both reforestation and shelter-belt planting beginning about 1925, new evidence from more critical experiments indicated the existence of climatic, edaphic, and biotic ecotypes in many other tree species. These included *Pinus banksiana* Lamb. (Hansen and Jensen, 1952); *P. resinosa* Ait. (Bates, 1930; Rudolf, 1948); *P. sylvestris* (Littlefield, 1939; Heimburger, 1945; Rudolf, 1950; Baldwin, 1953 and 1955; Hansen, 1954); *P. taeda* L. (Wakeley, 1944; Bercaw, 1955); *Picea abies* (Heimburger, 1945; Baldwin, 1949a); *Larix decidua* Mill. (Hunt, 1932; Baldwin, 1949b; McComb, 1955); *Juglans nigra* L. (White, 1926); *Fraxinus americana* L. (Wright, 1944a); *F. pennsylvanica* Marsh. (Meuli, 1936; Meuli & Shirley, 1937; Wright, 1944b); *Acer saccharinum* L. (Wright, 1949); and other species. Various degrees of ecotypic variation, sometimes clinal in nature and sometimes sharply defined, were evident for all of these species.

The great upsurge in forest tree improvement work starting about 1950 has resulted in the establishment of even more critical experiments. Already these tests are providing new or confirmatory evidence of ecotypic variation, either well defined or clinal in nature. Species included are the southern pines, *Pinus echinata* Mill. (Minckler, 1950; Wright, 1953b; Wakeley, 1955), *P. elliottii* Engelm. (Mergen, 1954; Wakeley, 1955), *P. palustris* Mill. (Wakeley, 1955), and *P. taeda* (Minckler, 1950 and 1952; Cummings, 1952; Zobel, 1955; Wakeley, 1955); as well as *P. banksiana* (Rudolf, 1955), *P. resinosa* (Hough, 1952; Wright, 1953b; Rudolf, 1955), *P. strobus* L. (Pauley *et al.*, 1955); *Populus deltoides* Bartr. and *P. trichocarpa* Torr. and Gray (Pauley and Perry, 1954), *P. tremuloides* Michx. (Wright, 1953b); *P. tremula* L. (Vloten, 1954); and *Juglans nigra* (Wright, 1954). Concurrently with this new work, the climatological aspects of seed source location are receiving increased attention in the West (Dick, 1955; Isaac, 1955) and South (Hooker, 1955).

Experimental Procedure

The data used in this study are from a cooperative project aimed at breeding blister rust (*Cronartium ribicola* Fischer) resistant and otherwise improved *Pinus monticola* trees (Bingham *et al.*, 1953). During the past 6 years controlled pollinations have been made among 45 trees selected for apparent resistance to blister rust. The selections occur within 8 different areas.

The controlled pollinations involved crosses between individual trees both on the same selection area and on different selection areas. Most of the crosses, however, were concentrated on several heavily fruiting individuals (also rust-resistant) termed "test trees." In addition to the controlled intraspecific crosses, wind-pollinated seeds were collected from each selection to the extent possible. Finally, wind-pollinated seeds were collected from control, nonresistant trees or from squirrel caches in the different areas; they are hereafter termed "control lots." The numbers of crosses, wind-pollinated lots, and control lots used in the present study are shown below according to the year in which the seeds were sown (hereafter termed "progeny trials"):

	Progeny trials (number)				
	1952	1953	1954	1955	Total
Controlled intraspecific crosses	41	9	31	85	166
Wind-pollinated lots collected from selections	17	10	18	39	84
Control lots	0	3	4	8	15

The eight selection areas are shown in Figure 1. All of the areas could be included in a circle about 30 miles in diameter. Two of them (Middle Fork and Gold Center) are only half a mile apart, but they involve greatly different growing sites, being on opposite sides of a major drainage (Fig. 2). Brief descriptions of the areas in decreasing order of site index (average height of dominant and codominant trees at age 50 years) follow.

1. Lower Elk Creek, Clearwater County. 3 selections. Elevation 3,000 feet. Almost flat bottomland. Average age 28 years. Site index 106. (This unusually high index is approximate, being determined by extrapolation of the site index alignment chart in Haig's bulletin, 1932.)

2. Crystal Creek, Benewah County. 15 selections. Elevation 2,850 feet. Topography is broken by minor drainages, but most of the trees are growing on practically flat to moderate slopes, where aspect is generally southwest-facing. Average age 32 years. Site index 90.

3. Upper Elk Creek, Clearwater County. 4 selections. Elevation 3,300 feet. Near base of moderate to steep, southeast-facing slope. Average age 26 years. Site index 88. (Observations of other characteristics of the site indicate that this index is overestimated, as sometimes results when the local site index chart is applied to very young stands.)

4. Middle Fork (St. Maries River), Shoshone County. 4 selections. Elevation 2,900 feet. Flat to moderate, north-facing, moist slope. Average age 53 years. Site index 67.

5. Emerald Creek, Latah County. 3 selections. Elevation 3,000 feet. Topography variable, slopes moderate to steep, generally facing north and south to southeast. Average age 38 years. Site index 67.

6. Soldier Creek, Benewah County. 2 selections. Elevation 2,700 feet. Steep, northwest-facing slope. Average age 71 years. Site index 57.

7. Gold Center, Shoshone County. 9 selections. Elevation 2,950 feet. Moderate to steep, south-facing, dry slope. Average age 38 years. Site index 55.

8. White Rock, Shoshone County. 5 selections. Elevation 5,000 feet. Moderate to steep, north-facing, moist slope or ridge-top. Trees here are noticeably affected by the rather high elevation, snow damage being common. Average age 50 years. Site index 48.

For purposes of analysis the 8 selection areas were divided into 2 groups: those comprising the 4 better growing sites and those comprising the 4 poorer sites, as judged mainly from their site indexes. Middle Fork and Emerald Creek, occurring midway in the whole group, had equal site indexes. However, since the mean annual growth rate of Middle Fork trees averaged somewhat greater than those of Emerald Creek (1.46 versus 1.33 feet per year), the former were included in the better-site group and the latter in the poorer-site group. Grouping of the areas made it possible to test statistically male-parent crosses on test trees groupwise. Such crosses were too few to permit similar tests between individual areas.

Progeny seeds were sown at a nursery at Spokane, Washington, each spring during the years 1952 through 1955, in a

randomized block design (Bingham *et al.*, 1953). When seedlings reached the age of 2 years they were outplanted at 3 localities: (1) Fernwood, elevation 2,750 feet, (2) Elk Creek, 3,000 feet, and (3) Randolph Creek, 4,400 feet (Fig. 1). At the time data for this experiment were summarized only lots comprising the 1952, 1953, and 1954 progeny trials had been outplanted.

Total heights and current height growth of the progenies were measured in the fall of each season. Most of the data reported here, however, were obtained in the fall of

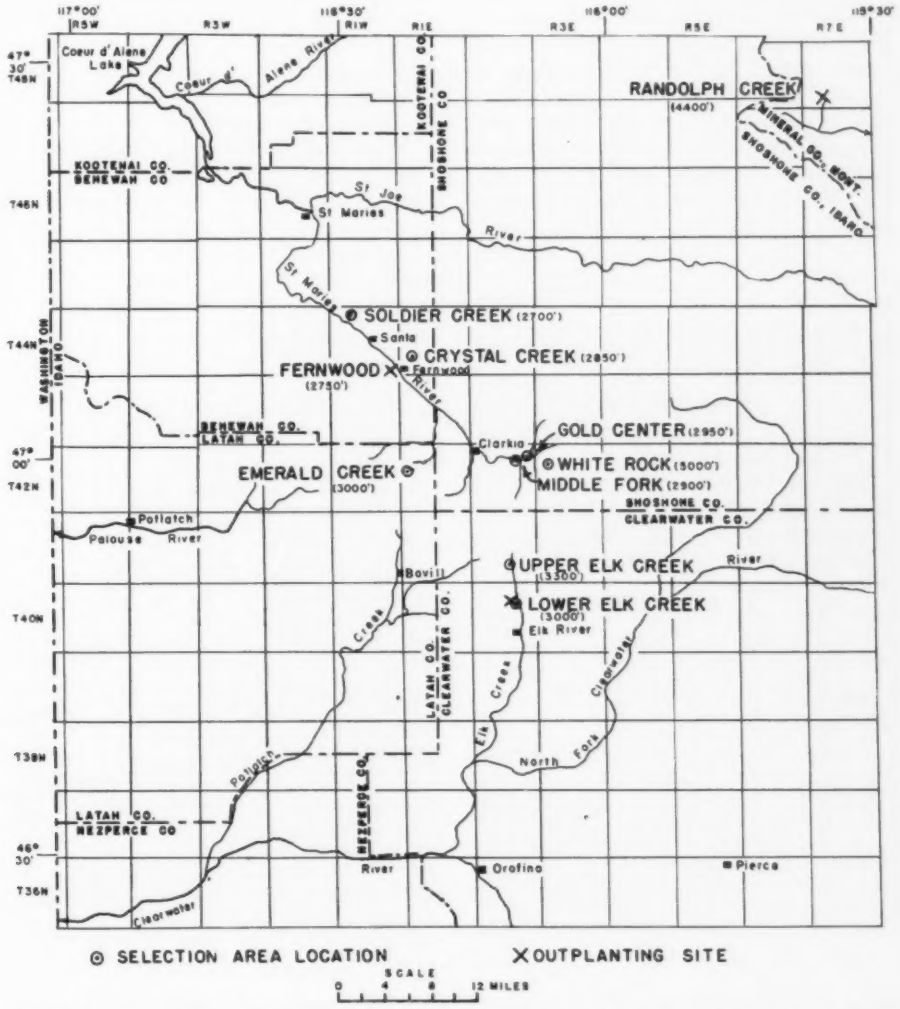
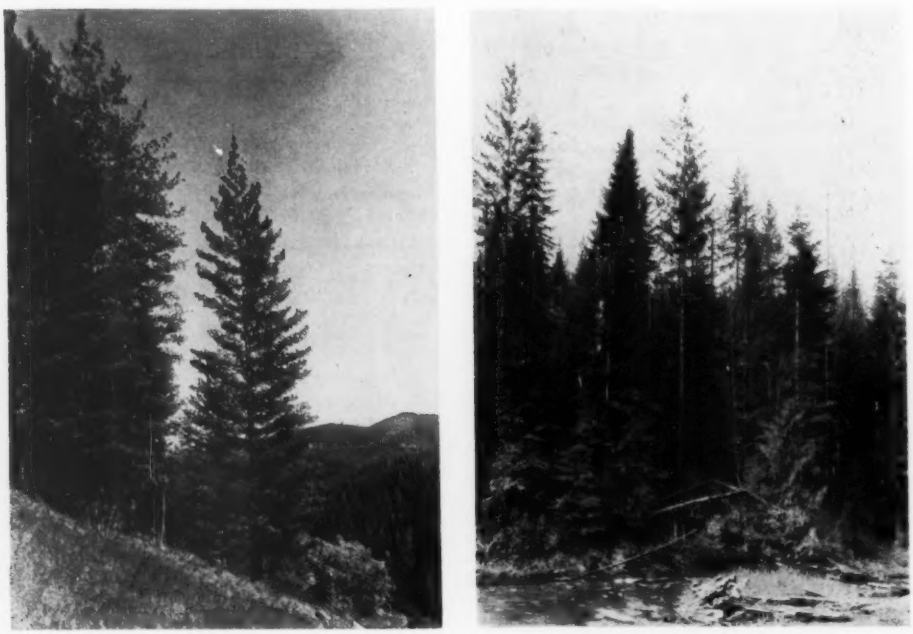


FIGURE 1. *Location and elevation of the eight selection areas and three outplanting sites, in northern Idaho and western Montana.*

1955. (Growth rates measured in the fall of 1956 on some of the 1953 progeny trial lots were used in a special study of differential response to planting site, described later.) Trees of the 1952 progeny trial were 4 years old at that time (1955); the 1953 trial, 3 years; the 1954 trial, 2 years; and the 1955 trial, 1 year.

Preliminary analysis showed that average total heights for the first 3 years were significantly correlated with seed weight. Current height growth measured on trees older than 1 year, however, was found to be largely independent of seed weight. Therefore, current growth rather than total height was used in analyzing data for lots older than 1 year in the fall of 1955 (the 1952, 1953, and 1954 trials). Height growth values for the 1-year-old lots (1955 trial) were adjusted to a common seed weight using the regression coefficient ($b = .0863$) computed from the 2 factors (Snedecor, 1946). The progeny growth rate data in all cases were averages of all trees in each progeny. The numbers of trees upon which they were based varied from 6 to 90, with an average of 48 per progeny.

Also for purpose of analysis, the progeny data were divided into 2 parts according to type of crosses: (1) progenies in which the selections were used as pollen parents on test trees and (2) progenies in which the selections were used as seed parents in crossing with test trees, plus wind-pollinated progenies of the selections. Wind-pollinated progenies were included with seed parent progenies because of their similarity



Gold Center *Middle Fork St. Maries River*

FIGURE 2. *The Gold Center and Middle Fork selection areas, one-half mile apart on opposite slopes of the same drainage. Open, dry conditions of Gold Center area contrast with dense, relatively moist conditions at Middle Fork.*

in respect to possible carryover of environmental effects as discussed below.

In evaluating differences between selection areas both groups of data were used. However, the "seed parent" data are considered the less reliable of the two because environmental factors of the site may possibly have an influence on seedlings indirectly through an effect upon nutrition or size of seed. As stated earlier, seed weight was taken into account in the analyses, but other factors such as nutrient content, if varying among selection areas, could affect seedling size. (Youngberg (1952) showed an effect of soil fertility upon chemical composition of seed.) Pollen, on the other hand, would not be likely to transport much environmental effect associated with the site from which it came.

Seeds from 116 of the 1955 lots were treated in osmotic pressure tests. The method used was patterned after that employed by Buchinger (1937) in wheat breeding. It consisted in first cold-soaking half the seeds of each lot in water and the other half in a 0.05 molar sucrose solution (1¼ atmospheres osmotic pressure) for a period of 9 days Then the seeds were placed in covered petri dishes and germinated on several sheets of filter paper kept moist throughout a 63-day germination period, with the same solution in which they were cold-soaked.

Percentage of seeds within a lot germinating in the sucrose solution was found to be significantly related to percentage of the same lot germinating in water. Therefore, percent germination in sucrose was adjusted to a common percent germination in water using the regression coefficient ($b = .2537$) computed from the two factors (Snedecor, 1946). Seed lots that germinated relatively well in the sucrose solution were considered as having higher osmotic pressures, or at least the ability to imbibe water from a more concentrated solution, than those germinating poorly in sucrose solution.

In April of 1956 an exploratory test of foliage dry-matter content was made on extra seedlings produced from the 1954 progeny trial lots. The trees used were not a part of the randomized block design mentioned earlier, the extra seed lots being sown in numerical order with no replication. Results of the test, however, showed no pronounced seedbed position effect and hence were considered sufficiently reliable for study. The lots used (comprising 11 wind-pollinations and 4 control lots) were 2 years old, all grown in the Spokane nursery. Foliage samples, varying from 2 to 36 grams of green material, were collected, weighed green, then dried in an oven at a temperature of 67° C. for 10 days. After drying they were weighed again and oven-dry weight was expressed as a percentage of green weight.

Results and Discussion

Variation in early progeny growth. Data assembled on the early growth rate of progenies of trees from the different selection areas suggest that differences in inherent growth rate exist between some of the areas. Table 1 shows the variation in growth rate of progenies obtained when trees of the different selection areas were used as pollen parents on the test trees. Use of pollen parents from the better sites usually resulted in faster growing progenies than pollen parents from the poorer sites. In determining the significance of differences for each progeny trial, the better-site means were tested against the poorer-site means by analysis of variance, using the individual progeny averages.

Table 2 shows the variation in growth rate among progenies of parents from different areas when they were used as seed parents, including crosses with test trees and wind pollinations. Here again, progenies of selections from the better sites grew more rapidly than those from the poorer sites. Where data were fragmentary (1952 and 1953 trials), nonsignificant differences were obtained.

To provide for a more clear-cut evaluation of the differences between selection

TABLE 1. Average height growth,[1] in feet, of progenies produced when selections from different site groups were used as pollen parents on test trees.

Site group	Test tree number 19	20	58	Significance
		1952 Progeny Trial		
Better sites	.236(13)	.241(7)	.251(9)	1 percent level
Poorer sites	.213(3)	.191(1)	.214(2)	
		1954 Progeny Trial		
Better sites	.100(6)	.110(2)		None
Poorer sites	.095(3)	.087(1)		
		1955 Progeny Trial		
Better sites	.107(10)	.112(6)	.112(7)	5 percent level
Poorer sites	.102(7)	.102(1)	.110(3)	

[1]The 1952 data refer to 4th-year growth; 1954, 2nd-year growth; and 1955, 1st-year growth, adjusted for seed weight. Figures in parentheses following a value show the number of crosses or wind pollinations on which it is based. The 1953 progeny trial was not included because no crosses involving pollen parents on test trees were represented.

TABLE 2. Average height growth,[1] in feet, of progenies produced when selections from different site groups were used as seed parents in crossing with test trees, and of wind-pollinated progenies.

Site group	Test tree number 19	20	58	59	Wind pollinations	Significance
			1952 Progeny Trial			
Better sites	.201(1)[2]	.....	.....	.....	.234(14)	None
Poorer sites	.212(1)	.....	.....	.....	.212(3)	
			1953 Progeny Trial			
Better sites	.....	.....	.....	.227(7)	.230(8)	None
Poorer sites	.....	.....	.....	.206(2)	.214(2)	
			1954 Progeny Trial			
Better sites	.094(1)	.100(2)	.....	.097(3)	.102(11)	1 percent level
Poorer sites	.082(4)	.088(4)	.....	.079(3)	.092(6)	
			1955 Progeny Trial			
Better sites	.098(4)	.108(6)	.102(4)	.105(8)	.109(24)	1 percent level
Poorer sites	.102(1)	.101(3)	.100(2)	.100(5)	.102(15)	

[1]Data given for each of the progeny trials are as follows: 1952, 4th-year growth; 1953, 3rd-year growth; 1954, 2nd-year growth; 1955, 1st-year growth, adjusted for seed weight.

[2]Figures in parentheses following a value show the number of crosses or wind pollinations on which it is based.

areas and site groups, each individual selection was rated for over-all progeny performance. In order to do so, it was first necessary to level off the differences between progeny trials, which were due largely to differences in age.

Data of the 1953, 1954, and 1955 trials were brought to the level of the 1952 trial on the basis of performance of "standard progenies" (progenies that were repeated in one or more years). Simple proportions derived from the standards were applied to all other progenies. Finally each selection was evaluated by averaging its progeny values from the pooled data (crosses on test trees and wind pollinations of all trials). The results showed that progenies of selections on the better sites grew an average of 10 percent faster than those of selections on the poorer sites. The greatest difference among individual areas occurred between Upper Elk Creek and White Rock, the former averaging 15 percent faster growth than the latter. An analysis of variance of these data showed that both the differences in average growth rate between individual areas and between site groups were highly significant.

As a further check upon the apparent relationship of site and progeny growth rates the correlation between these two variables was computed. Site indexes for all selection areas and the weighted mean progeny growth rates derived from both selections and controls were used. The correlation coefficient was found to be +.87, significant at the 1 percent level.

Results presented thus far have dealt with average growth rates irrespective of planting site. As mentioned earlier, 2 of the outplanting sites were at relatively low elevations (Fernwood, 2,750 feet and Elk Creek, 3,000 feet) while the third was at a relatively high elevation (Randolph Creek, 4,400 feet). Since some of the progenies had parents from high elevations, the possibility of differential response to outplanting site was checked. As expected, all progenies grew considerably more rapidly at the 2 lower elevations than at the high elevation. More important, however, progenies of high-elevation parents grew relatively better at Randolph Creek (high elevation) than did those of low-elevation parents.

Data leading to the latter conclusion are shown in Table 3. In this analysis only the 1953 progeny trial (outplanted 2 years) could be used, since progenies of other trials either did not involve high elevation lots or had not recovered from transplanting effects.

In Table 3 average current fourth-year growth at Randolph Creek (the second year after outplanting) is shown along with average second-year total height in the nursery. Although progenies of White Rock parents (high elevation) were shorter at time of outplanting, they grew more rapidly in their fourth year than those of the two low elevation sources. A single control lot (Randolph control) originating from seed collected in the vicintiy of the planting site performed in the same manner as the White Rock lots. Analysis of variance showed that the differential re-

TABLE 3. Differential response in growth rates of progenies of high versus low elevation sources when outplanted at a high elevation site. Data from 1953 progeny trial lots, Randolph Creek outplanting.

Seed source	Total height at 2 years (in nursery)	Height growth during 4th year (at Randolph Creek)	Basis, lots
	Feet	*Feet*	*Number*
Low elevation lots:			
Crystal Creek	.207	.139	8[1]
Elk Creek	.207	.142	3[2]
High elevation lots:			
White Rock	.153	.164	5[3]
Randolph Creek	.171	.172	1[4]

[1]Wind-pollinated lots from 6 selections, plus 1 within-area cross and 1 control lot.
[2]Wind-pollinated lots from 2 selections, plus 1 within-area cross.
[3]Wind-pollinated lots from 2 selections, plus 2 within-area crosses and 1 control lot.
[4]One control lot.

sponses were significant at the 1 percent level.

Variation in apparent osmotic pressure of seeds. Variation in the apparent osmotic pressure of progeny seeds of trees from different selection areas produced further evidence of inherent differences between trees growing in the different areas. Values obtained for individual seed lots varied considerably even within areas, possibly due to inherent individual tree variation but also to small samples in some instances. In spite of the unexplained variation there appeared to be a fair degree of consistency among selection areas.

Lots were first averaged by individual seed parents and pollen parents and then by selection areas. The area means of apparent osmotic pressure (expressed as the percent of seeds germinating in 0.05 molar sucrose, adjusted for percent germination in water) are given by sex of parents and kinds of seed lots in Table 4. The data show a rather high degree of consistency of selection area averages by seed parents, pollen parents, and wind pollinations of selections and controls, as well as large differences between areas. For example, osmotic pressures of controlled pollinated progenies involving at least one Crystal Creek selection were low, no matter whether the selections were used as seed parents or pollen parents. Similarly, wind-pollinated progenies of selections in Crystal Creek and the control lot for that area had low values. Some discrepancies occurred, as exemplified by the values for Soldier Creek, but they are mostly where the numbers of selections involved in the means are few.

Unfortunately crosses of pollen parents from different areas on test trees were insufficient in number to permit a test of pollen parent effects similar to the test applied for growth rate. However, an analysis of variance of the pollen parent means as derived above showed the differences between selection areas to be significant at the 5 percent level. Including selection means derived from all progenies (all crosses and wind pollinations), differences between selection areas were significant at the 1 percent level.

Finally, the correlation of progeny seed

TABLE 4. Average 63-day percent germination of seed of selections and control trees in 0.05 molar sucrose solution,[1] by type of progeny and selection area.

Selection area	Controlled pollinated progenies of selections used as:				Wind-pollinated progenies of selections		Averages, all progenies of selections		Wind-pollinated progenies of control trees[2]	Averages, all progenies[3]
	Seed parents		Pollen parents							
	Germination	Basis, selections	Germination	Basis, selections	Germination	Basis, selections	Germination	Basis, selections	Germination	Germination
	Percent	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Percent*
Lower Elk Creek	5.3	3	11.2	1	2.8	3	6.7	3	5.8	6.1
Crystal Creek	8.7	9	7.3	12	5.4	13	7.3	15	4.0	6.5
Upper Elk Creek	19.0	2	13.7	4	9.8	2	15.5	4	15.0	15.2
Middle Fork	6.6	2	5.2	4	3.6	4	5.2	4	8.2	6.9
Emerald Creek	22.9	1	16.2	1	.....	0	19.6	2	6.4	10.2
Soldier Creek	.....	0	6.6	2	18.2	1	9.4	2	7.8	8.6
Gold Center	10.2	5	12.8	4	13.2	6	12.7	7	13.4	13.0
White Rock	11.2	3	16.8	3	15.8	5	15.8	5	17.6	16.7

[1]Adjusted for percent germination in water as described in text. Osmotic pressure of 0.05 molar sucrose solution is approximately 1¼ atmospheres.

[2]Mixtures of seed collected from 5 control trees chosen at random within selection areas.

[3]Average based on all progenies of selections (weighted by number of selections) and progenies of control trees (weighted by number of trees involved in the control lots).

osmotic pressure with site index was tested and the resulting correlation coefficient, —.50, was found to be nonsignificant. Still, among those areas having relatively low osmotic pressures (Elk Creek, Crystal Creek, Middle Fork, and Soldier Creek) all but the last are in the better-site group. Similarly, among areas showing relatively high values, all but upper Elk Creek are in the poorer-site group. The nonconformance of Upper Elk Creek may have been due to inaccuracy of site index determination for this area. Although there appears to be some tendency for low seed osmotic presssure to be associated with high site index, further testing would be necessary to prove whether or not such a relationship exists.

Variation in foliage dry matter content. The small test of dry matter content of foliage showed that progenies from White Rock (high elevation) averaged higher in dry matter content than those from lower elevations (Table 5). The mean difference, 1.4 percent, was significant at the 1 percent level. As stated earlier, the foliage was collected in April 1956—prior to breaking of dormancy—from trees of the same age (2 years) growing at a single nursery. Whether differences among areas of similar elevations occur could not be determined from this test. The differences between high and low elevations certainly seem real, however, and in harmony with results reported by Langlet (1936). He showed that foliage of progenies from northern provenances possessed higher dry matter content than those from southern origins. Apparently the same is true for high versus low elevations in western white pine.

TABLE 5. Dry matter content of foliage taken from 2-year-old wind-pollinated progenies of selections and control trees from low versus high selection areas, 1954 progeny trial.

Low elevation areas		High elevation area	
Lot	Dry matter content	Lot	Dry matter content
	Percent		*Percent*
Lower Elk Creek		*White Rock*	
59 × wind	38.2	54 × wind	38.1
62 × wind	36.6	63 × wind	39.9
Control[1]	37.2	69 × wind	38.8
		70 × wind	39.0
Crystal Creek		Control[1]	38.6
18 × wind	36.9		
21 × wind	37.3		
25 × wind	37.2		
58 × wind	38.2		
Control[1]	38.3		
Middle Fork			
30 × wind	37.4		
Gold Center			
Control[1]	37.8		
MEAN	37.5	.....	38.9

[1]Mixtures of seeds from rust-infected trees chosen at random within selection areas.

Theoretical Aspects of Ecotype Formation

The apparent existence of distinct ecotypes as little as one-half mile apart in continuous *Pinus monticola* stands is interesting, considering that Pauley *et al.* (1955) found only clinal variation among local *P. strobus* stands. Clinal variation within local populations seems to be the usual case with intensively studied eastern species including *Fraxinus americana* (Wright, 1944a), *F. pennsylvanica* (Wright, 1944b), and perhaps other species including *Juglans nigra* (Wright, 1954) and the southern pines (Rudolf, 1955).

One case of apparent existence of sharply defined ecotypes in isolated populations within the species *Acer saccharinum* within a 100-mile radius is reported by Wright (1949). Wright (1953b) points out that gaps of as little as one-half mile, if they exist in the population, would probably be adequate for formation of distinct ecotypes, and his pollen dispersion studies (1952 and 1953a) bear out this minimum distance for certain species. Thus most of the evidence indicates that a pronounced pollination or seed dispersion barrier accompanies formation of distinct ecotypes in the East.

Within the "same forest" in Russia,

Piatnitsky (1953) found forms of *Quercus robur* L. that flushed late growing on moist, northerly slopes and producing drought-intolerant seedlings; on the other hand, he found forms that flushed early growing on dry, southerly slopes and producing drought-tolerant seedlings. Similarly, in the midwest Hall (1955) found that populations of *Juniperus virginiana* L., growing on the droughty shallow soil of open glades were distinct from those found on deeper soils of old fields less than a mile away. Hall attributed the formation of the two distinct populations to strong natural selection as a result of high seedling mortality in the open glade.

It appears that somewhat similar selection pressures exist in much of western inland North America and that they may result in differentiation of ecotypes within relatively continuous stands in western species. For instance, the area sampled by Pauley *et al.* (1955) in discerning clinal variation in *Pinus strobus* (New England, New York, Virginia, Michigan, and Pennsylvania) is characterized by moderately abundant summer rain. The North Idaho area showing sharp and localized ecotypic variation in *P. monticola* as sampled in this study is characterized by summer drought. The tabular summary below shows the differences in summer precipitation.

Locality	*Precipitation (inches)*			
	July	Aug.	Sept.	Total
Range of *P. strobus*, 53-year avgs. (Anonymous, 1941)	3.67	3.58	3.32	10.57
Range of *P. monticola*, 19-year avgs. (Hanna, 1937)	0.76	0.94	1.64	3.34

Furthermore, western inland topography is rough, broken, and with opposing slopes (north and east versus south and west), usually representing widely different microclimates. Moreover, the valley bottoms (i.e., the middle ground out from which might radiate forms intermediate in survival ability) are often narrow and limited in their usefulness as a habitat for *P. monticola* because of unfavorable soil type or excessive soil moisture. They are most frequently occupied by herbaceous and brushy plants, if not by trees of other species.

Under these conditions it is logical to assume that differences in seedbed moisture occurring between opposing north and south slopes might constitute a considerable barrier to gene dissemination. The barrier in this case would not act through mere isolation and resulting failure of pollen exchange between slopes, but rather through failure of seedlings having moist-site pollen parents to become established on dry sites and seedlings having dry-site pollen parents to attain dominance and survive to seed-bearing age on moist sites.

The reader will recall that the progeny seeds of the moist Middle Fork area averaged 5.2 percent germination in sucrose solution (apparently low osmotic pressure) while those of Gold Center, half a mile upstream but on the opposing dry south-facing slope, averaged 13.0 percent. It is conceivable that seeds having high osmotic pressures are more capable of germinating and surviving on drier sites. If so, it is likely that seeds borne on dry-site trees but pollinated by trees on a nearby moist site are less capable of survival on the dry site than seeds having both parents from the dry site. Went's (1954) observations on the importance of germination on the establishment of communities and Piatnitsky's (1953) report on the drought hardiness of seedlings from more or less opposite slopes support this theory.

Juvenile growth rate data from this study further support the theory in regard to establishment of seedlings with dry-slope antecedents on moist slopes. The following tabulation shows average current height growth (adjusted for age) of controlled pollinated progenies of crosses from within and between the Middle Fork and Gold Center areas; also corresponding wind-pollinated progenies.

	Current growth (feet)	*No. of crosses*
Moist site × moist site:		
Middle Fork × Middle Fork	0.248	3
Middle Fork × wind	0.237	4
Moist site × dry site and vice versa:		
Middle Fork × Gold Center	0.237	1
Gold Center × Middle Fork	0.242	2
Dry site × dry site:		
Gold Center × Gold Center	0.222	2
Gold Center × wind	0.222	6

Among controlled pollinated progenies, those with both parents of dry slope origin are the slower growing. The inter-slope progenies meet theoretical expectations in that they are intermediate in growth rate between those of the two intra-slope populations. It is reasoned that eventually they would be largely eliminated from moist slopes, being unable to survive when in competition with the faster growing moist slope × moist slope trees. There is a good possibility that selection pressure discriminates against infiltration of genes from trees adapted to radically different although adjacent sites, as when pollen exchange occurs between opposing cool-moist and hot-dry slopes.

Application of Findings

Knowledge of the existence of broad races or ecotypes has long been used to emphasize the desirability of obtaining natural regeneration where possible, and if not, the need for care in selection of seed collection areas and the location of planting sites. Results of the present study show that there should be further investigation of the relation of the factors studied in establishment and survival of plantations and their subsequent growth.

Will it be necessary to envisage a greater refinement than heretofore, encompassing variation in site moistness and exposure along with the customary latitudinal, longitudinal, and altitudinal provenance zones? If so, will the cost of such refinement in seed collection be prohibitive? Should differences in site other than altitudinal be considered in breeding efforts and subsequent establishment of seed orchards? Additional progeny tests including all the putative ecotypes and different planting sites, together with followup on growth of progenies beyond the juvenile stage, are needed to answer these questions.

Conclusions and Summary

Controled breeding work with *Pinus monticola* Dougl. conducted during the years 1950-55 has produced evidence that ecotypes of a very local nature exist. The evidence is based upon 166 controlled pollinations made among 45 trees (selected for apparent resistance to blister rust) growing in 8 areas. In addition to the controlled pollinations, wind-pollinated seed were collected from the selections and from other nonresistant trees growing on the different areas. Certain selection areas, though in one case as little as one-half mile apart, represented considerably different environments.

Growth rates of the parent trees and their progenies up to 4 years of age were measured. Seeds of 116 progenies were subjected to osmotic pressure tests, and foliage dry matter content was measured on 15 progenies. Results were as follows:

1. Progenies of trees from the better sites (moist, low elevations) grew more rapidly, on good planting sites, than those of trees from poorer sites (dry slopes or high elevations).
2. Progenies of trees from high elevations grew relatively more rapidly when outplanted at a high elevation than progenies of low elevation sources.
3. Progenies of trees from high elevations had more foliage dry matter content than those of low elevations.
4. Progeny seeds from different selection areas exhibited differences in apparent osmotic pressure. There was some tendency for low osmotic pressure to be associated with high site index, but further testing would be needed to prove this relationship.

Some hypotheses regarding the forma-

tion of truly local ecotypes are discussed. The conclusion is that where topography is highly variable and growing-season moisture is a critical factor, selection pressures such as seedling establishment and growth rate discriminate against infiltration of genes from trees adapted to radically different although adjacent sites. The authors recommend further investigation of the relation of the phenomena studied to the establishment and survival of plantations and their subsequent growth.

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Methods of Surveying Infestation of the Black Hills Beetle in Ponderosa Pine

BY
FRED B. KNIGHT

THE BLACK HILLS BEETLE (*Dendroctonus ponderosae* Hopk.) is the most serious insect enemy of ponderosa pine (*Pinus ponderosa* Laws.) in the central Rocky Mountain region (Beal, 1939; Blackman, 1931). This insect is extremely aggressive; during outbreaks, it attacks and kills vigorous, healthy trees. Much has been learned about its biology and methods for control; consequently, outbreaks can now be stopped by use of artificial control methods (Massey *et al.*, 1953). But more ecological research is needed so that outbreaks can be predicted and prevented.

Need for Surveys and Survey Improvements

The Black Hills beetle may kill thousands of ponderosa pines in a single year. During the period from 1895 to 1908 between 1 and 2 billion board-feet were killed in the Black Hills alone. Between 1950 and 1955 an estimated 58,000 trees were killed on the Roosevelt National Forest and over 46,000 were killed on the Bighorn National Forest. This destruction shows the importance of the insect as a primary pest of ponderosa pine. The infestations on the Roosevelt and Bighorn National Forests were terminated by use of chemical control measures.

Agencies that manage these stands need reliable estimates of the number of infested trees when they plan their control projects. Funds and manpower determine the amount of survey work that goes into obtaining these estimates.

The accuracy for each survey should be known and expressed along with the estimate so that the managing agency can interpret the information readily. Then, should the accuracy or confidence limits of the estimate be unsatisfactory, it is necessary to know how much additional surveying is needed to obtain the desired results. This can be done only if there is thorough knowledge of proper survey methods and reliability of the data.

Surveys

The Black Hills beetle does not attack trees in any particular pattern within a stand (Knight and Yasinski, 1956). The attacks generally are made on groups of trees rather than on random individuals. Conceivably the attack on the first tree in a group may be at random, but if so, this is of little value in planning surveys. In an endemic situation the infested trees may be scattered individuals or widely spaced small

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groups. When conditions favor beetle-population increases so that epidemics develop, these groups expand and new groups or individually infested trees appear throughout the stand. As the infestation increases, the groups enlarge and become more numerous until they coalesce.

This grouping of infested trees suggested a type of ground survey for estimating numbers of infested trees: the small plot or strip commonly used in timber surveys. This type was adopted for the early Black Hills beetle surveys. Various methods, such as ½-acre to 1/10-acre plots along cruise lines and 1-chain and ½-chain-wide strips, were used. According to reports of the supervisors who used them, all methods generally gave satisfactory estimates. Occasionally, a particular survey resulted in extremely poor estimates. These poor estimates were frequent enough to suggest that perhaps the methods were at fault. Commonly overlooked was the fact that surveys are made up of samples, and that among many samples of items a measurable portion is not representative of the total population. Frequently the surveyors themselves did not know why their estimates were so divergent.

This leads to two questions that research on ground surveys should answer:

1. Which of the several methods of strip- and line-plot surveys successfully used in the past requires the least expenditure for estimates of a desired accuracy?
2. How much of the area must be covered to obtain an estimate that has the desired accuracy?

Since the foliage of currently infested ponderosa pine is green, counts or estimates cannot be made by aerial observations. Aerial surveys measure only old kill (insect-abandoned trees) because only trees with discolored foliage can be detected from the air. The method used before aerial surveys took advantage of the rough terrain; the scope of an infestation and an estimate of damage was obtained by observing from vantage points. Of course, many areas were difficult to see.

Today very accurate maps of the areas to be surveyed by field crews can be delineated from the air. In addition, estimates of the infested trees killed the previous year can be obtained by aerial surveys made in July or August. Accurate estimates of these losses can be made by observers who count and record all the straw-colored trees (trees infested the previous year) on wide strips during systematic flights over the timber. Accurate estimates of the number of straw-colored trees can also be obtained from colored aerial photographs of the entire infested areas. Transparencies of the photographs are examined with a mirror-stereoscope on a light table. Trees with dying foliage can then be readily observed and tallied.

Comparison of Five Survey Methods

Five survey methods consisting of 3 plot sizes and 2 strip widths have been compared to determine the most efficient method for Black Hills beetle surveys. Two analyses were made:

1. A study of accuracy of estimates.
2. A study of time required to cover a unit area.

The five methods were:

1. 1/10-acre plots at 2-chain intervals along parallel cruise lines.
2. 1/5-acre plots at 2½-chain intervals along parallel cruise lines.
3. ¼-acre plots at 2½-chain intervals along parallel cruise lines.
4. Parallel cruise lines of ½-chain width.
5. Parallel cruise lines of 1-chain width.

In general the five methods produced approximately the same results for any one tract when the same number of cruise lines were used. This was shown to be true even though some tally acreages were two times as large as others. The larger acreages of tally obtained from wider strips or larger plots did not improve the accuracy of the estimates. Although no one of the five methods proved superior, the results favored

the ½-chain-strip method. Therefore, the method producing the greatest number of cruise lines within the time allotted for the survey is the logical and recommended method to use in ground surveys of Black Hills beetle infestations.

In terms of time required to run a given length of cruise line, the 1/10-acre-plot method or the ½-chain-strip method can be run significantly faster than any of the other three methods. A regression equation was developed with which the expected time per 10 chains of cruise line was calculated for various patterns of plots or strips. This equation is:

$$Y = 14.31 + 11.71\ (X - 0.76)$$

where

X = acreage of tally in 10 chains of cruise line.

Y = calculated time in minutes to cruise 10 chains of line.

Because inexperienced personnel can be trained more quickly to obtain more accurate results with the ½-chain-strip method, it is preferred to the 1/10-acre-plot method.

Sampling Error

After the most promising of the five methods was determined, the one selected (½-chain strips) was applied to various acreages at various rates of coverage. Sampling errors were computed, the factors affecting sampling error were determined by regression analysis, and tables were constructed to show predicted sampling error.

In this study, all infested trees were plotted at a scale of one inch to one chain. Nine maps of infested areas were utilized for surveys run in the office (Table 1). Seven of these maps were constructed in 1951, two in 1953. Two additional larger maps were obtained by combining the seven (1951) maps as one area and the two (1953) maps as another. This study was so extensive that the costs of actual field surveys would have been prohibitive. Sampling errors obtained in the more precise office surveys may have differed slightly from field surveys. Since inaccuracies in field surveys are largely compensating, their effect is small on sampling error and negligible on regression analyses.

To obtain valid sampling errors, the estimator selected random samples so that all parts of each area had an equal chance of being observed. This was done with the understanding that the procedure should be applicable to field use. The areas were broken into blocks of varying width according to the percentage of area covered: where coverage was 20 percent, block width was 5 chains; 10 percent, 10 chains; 5 percent, 20 chains; and 2.5 percent, 40 chains. The exact percentages of coverage listed were not achieved because of variations in the shape of the areas, but they were very close.

These blocks were positioned in reference to natural boundaries as would be done in the field. The lengths of blocks were not equal over all areas although they were, if possible, made equal within each area. In small areas an attempt was made to obtain as many blocks as could be justified. On the larger areas the blocks were plentiful without attempting further division. Four block widths were used on each area. Two cruise lines ½ chain in width were chosen at random within each block.

Since each map showed the location of each infested tree for two consecutive years, each map was used for two surveys. For example, one survey would be concerned

TABLE 1. Acreages and numbers of killed trees in 11 areas.

Area	Acres	Killed trees			
		1949	1950	1951	1952
	No.	*No.*	*No.*	*No.*	*No.*
1	417	232	672	.....	.....
2	314	1,495	748	.....	.....
3	366	123	245	.....	.....
4	90	30	38	.....	.....
5	292	158	337	.....	.....
6	74	122	148	.....	.....
7	90	48	342	.....	.....
8	1,189	.....	.....	584	306
9	1,539	.....	.....	569	700
10 (1–7)	1,643	2,208	2,530	.....	.....
11 (8–9)	2,728	.....	.....	1,153	1,006

only with the trees attacked in 1949. A second survey, using a completely new set of random positions for the cruise lines, would be concerned with the trees attacked in 1950. Thus, the positions of different random cruise lines were selected from tables of random numbers for each block width, each year of attack, and each map. Hence, for 4 block widths, 2 years of attack, and 11 maps, 88 observations were made. Three observations were dropped because no tally was recorded. The study, therefore, was based upon 85 surveys of varying acreages, infestations, and survey coverages.

Data recorded on each of two cruise lines within each block were length in chains and number of killed trees. The variance of the total number of trees killed in the two lines in each block was computed. These were weighted according to the lengths of the two lines, and a finite correction was applied to the variance for each block. The block variances were totaled to give a variance for the total tally of killed trees on an area. The standard error was multiplied by a t value (at the 2 to 1 level of accuracy) based on degrees of freedom equal to the number of blocks.

The sampling errors were not comparable. For comparison purposes all the sampling errors were converted to percentages by dividing by the total number of tallied trees.

The variances of the various block widths were studied so that some idea of proper weighting would be available before attempting any regression. Changes in block width apparently caused no changes in variance (Table 2), but the individual area variances fluctuated greatly for any block width. The variance comparisons suggested that each observation be given a weight of one.

TABLE 2. Average variances and standard deviations of the block tally for the various block widths.

Block width (chains)	Variance s^2_y (W = 1)	Standard deviation (W = 1)
5	6.8711	±2.62
10	9.8762	±3.14
20	9.7555	±3.12
40	7.3801	±2.71

Regression Analysis

A regression analysis (Schumacher *et al.*, 1942) by the method of least squares is best suited to the problem of determining the causes of variations in sampling errors and their significance. The dependent variable (y) is the sampling error converted to percentage form. The independent variables affecting the y's as measured in the study are:

X_1 = the acreage of the area.
X_2 = the percentage of area surveyed.
X_3 = the number of infested trees per acre.
$X_4 = X_1X_2$.

Two factors were considered in setting up the model. First, because the dependent variable approached a lower limit with the higher values of the independent variables, these were converted to reciprocals in order to include the asymptotic character of the relationship. Second, the fit of the regression was considered. The regression as computed with the straight reciprocal resulted in a poor fit with a tendency toward low estimates of the dependent variable at the lower values of the independent variables. The reciprocal of the square roots of the independent variables resulted in a good fit.

The model was designed for the limits of the data; extrapolations are not advisable. A model could be developed that would pass through the zero point as it theoretically should for a 100 percent survey. However, for the purposes of this study and in view of field restrictions, it was not necessary to adapt to the extreme values. For example, more than a 20-percent survey would be prohibitive in cost; likewise, an area containing no infestation

would not be surveyed. The final model is:

$$Y = a + \frac{b_1}{\sqrt{X_1}} + \frac{b_2}{\sqrt{X_2}} + \frac{b_3}{\sqrt{X_3}} + \frac{b_4}{\sqrt{X_4}}$$

All variables were retained in the final regression equation. Although X_4 was not significant at the 5-percent level, its effect was of significance high enough to warrant retention. The regression equation is:

$$Y = \frac{350.00}{\sqrt{X_1}} + \frac{80.18}{\sqrt{X_2}} + \frac{27.14}{\sqrt{X_3}} + \frac{959.20}{\sqrt{X_4}} - 51.4481$$

As a means of testing the fit of the regression, the dependent variable Y (sampling error in percent) was calculated from the field data for each of the 85 observations. This value was compared with the observed sampling error in percent (y). The deviations ($y - Y$) were computed for the 85 observations. These deviations were grouped into broad classes and plotted against each of the four independent variables. The plotting of the 85 observations of ($y - Y$) showed that the values were normally distributed about the zero mean, and the variation of the signs of the deviation was random.

As a final test to show the validity of the ½-chain-strip method, the actual errors (in percent) of the estimates were computed by dividing the estimates into the differences betwen the 100-percent counts and the estimates. The actual errors were compared with the sampling errors to determine the number of actual errors larger than sampling errors. Since the sampling errors were computed at the 2 to 1 level of accuracy, 2 out of 3 of the actual errors should be smaller than the sampling errors. Sixty-two of the 85 observations of actual error of the estimate were less than the sampling errors. This is better than the 2 out of 3 expected.

The regression analysis is of value in a more practical way. Table 3, which is of very great value in planning surveys, was constructed by inserting the various values of the independent variables into the equation. The degree of accuracy and the coverage needed to obtain this accuracy can be predicted from this table. Splitting of areas into small survey units can be avoided because there will be fewer requests for surveys on such small units. Proof is available to show that such surveys will cost perhaps 20 times the cost of a survey of the same accuracy on the area as a whole.

Two factors must be known approximately before the tables can be used. Both can be obtained by an aerial survey designed to delineate the area: (1) the acreage, and (2) the intensity of the infestation. The tree-per-acre figure need only be an estimate of trees (red-tops) infested the previous year, or this number may be obtained from the previous year's survey.

The areas considered in the tables do not exceed 3,000 acres. Extrapolations show that for 5,000 acres or more a 2.5 percent survey is ample for most situations. Areas larger than 5,000 acres probably would not be surveyed without dividing them into smaller blocks. In fact, areas of more than 3,000 acres seldom are surveyed as a single block.

Additional Research Needed

Although this research indicates a good method for ground surveys of Black Hills beetle infestations, additional studies in two broad fields are needed. One that warrants additional research is the correlation of ground surveys with aerial surveys. Even though accurate estimates of straw-colored

TABLE 3. Percent sampling error for various acreages, by infestation rate and survey coverage.

Infested trees per acre (number)	Survey coverage	Sampling error[1] when area in acres is— 100	250	500	1,000	1,500	2,000	3,000
	Percent				*Percent*			
0.25	10.00	----	----	----	49	45	43	40
	20.00	----	----	46	39	35	33	31
0.50	5.00	----	----	----	47	43	40	37
	10.00	----	----	42	33	29	27	24
	20.00	----	40	30	23	19	17	15
0.75	2.50	----	----	----	----	----	----	48
	5.00	----	----	----	40	36	33	30
	10.00	----	46	34	26	22	20	17
	20.00	----	33	23	16	12	10	8
1.00	2.50	----	----	----	----	----	48	44
	5.00	----	----	46	36	32	29	26
	10.00	----	42	30	22	18	16	13
	20.00	50	29	19	11	8	6	----
1.50	2.50	----	----	----	----	46	43	39
	5.00	----	----	41	31	27	24	21
	10.00	----	37	25	17	13	11	8
	20.00	45	24	14	6	----	----	----
2.00	2.50	----	----	----	49	43	40	36
	5.00	----	----	38	28	24	21	18
	10.00	----	34	22	14	10	8	5
	20.00	42	21	11	4	----	----	----

[1]Sampling errors greater than 50 percent are not included in the table. Such errors are not considered acceptable.

Confidence of sampling errors is at the 2 to 1 level; i.e., 2 times out of 3 the error should be less than that shown in the table.

pines can be made from the air, the limited tests for converting the straw-color count (last year's infested trees) to number of green (currently) infested trees have been discouraging. The necessary ground work has been as much as, and in many places more than, that required for the usual ground survey. Studies should be continued until a positive result is obtained to show whether the method is feasible.

The second field of study concerns insect populations. This is a large field and an immense amount of research is needed. Only a thorough knowledge of why populations of insects fluctuate will answer many questions concerning the epidemiology of outbreaks. Only through knowledge of these fluctuations can the results of any survey be interpreted most intelligently. Basic to a knowledge of insect ecology is the understanding and interpretation of population fluctuations, and their causes. Population studies will indicate whether an infestation is static, growing, or lessening. Population dynamics are extremely important and should be considered in the classification of infestations. Aerial counts of straw-colored trees along with predicted changes based on insect population counts show promise as an appraisal survey meth-

od. Population studies must be continued for some time before such a method can be applied in the field.

Summary

The research reported here, as well as the experience of foresters and entomologists, has led to the recommendation of a ground survey method (½-chain strips) for estimating numbers of ponderosa pine infested by the Black Hills beetle.

Experience in handling infestations since the early part of the century has shown that the type of survey utilizing continuous narrow strips or lines of small plots is reliable for estimating numbers of infested trees. The irregular groupwise pattern in which trees are attacked makes it important that sampling be as representative as feasible.

Tests were conducted in which five methods (3 plot sizes and 2 strip widths) were compared to determine which might produce the best estimates. When equal numbers of lines were cruised in areas of known numbers of infested trees, it was found that the estimates resulting from the use of any one method were no better than estimates from any of the other methods. This was true despite the fact that the acreage of tally was as much as two times greater in some methods as in others. It was concluded that the method by which more lines could be cruised to get a more representative coverage would produce the best estimates.

A time study of the five methods showed that the ½-chain-wide strip and 1/10-acre-plot methods were significantly faster in covering distance than the other three methods (1/5-acre and ¼-acre plots and 1-chain-wide strips). The ½-chain-strip method is preferable to the 1/10-acre-plot method because of better accuracy in field use.

Eleven areas containing known numbers of infested trees were cruised, using 4 intensities of coverage and the ½-chain-wide-strip method. Sampling procedures were completely random. A regression analysis showed that sampling errors of the surveys are influenced significantly by these factors: (1) the acreage, (2) survey coverage, and (3) the number of trees infested. From this regression, tables were developed to show predicted sampling errors for various combinations of the significant variables. These are useful in planning surveys where a specified confidence interval is desired.

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Stain Technique for Rapid Diagnosis of Rust in Southern Pines

BY
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In studies of the morphology and host-parasite relationships of *Cronartium fusiforme* and *C. cerebrum* on southern pines, a rapid technique has proved useful in differentiating the parasites from the host tissues.

Several workers have reported stain combinations for differentiating rust mycelium in pine tissue. Colley (1917, 1918) stained sections of white pine with safranin and light green, Heidenhain's iron-alum hematoxylin, and safranin and Delafield's hematoxylin to diagnose blister rust. Gram and Jorgensen (1952) used a combination of fast green FCF or light green SF and alcoholic safranin to differentiate hyphae in tissue of 13 species of hard and soft woods in hand sections. The combination of orseillin and aniline blue has been used extensively for differentiation of rust fungi in pine. Hutchinson (1935) and McKenzie (1942) utilized Strasburger's orseillin and aniline blue combination to study and trace the mycelium of a *Peridermium* in pine. In work with the Woodgate *Peridermium*, True (1938) found acidulated aqueous solutions of orseillin BB and aniline blue very useful in distinguishing between the parasite and the host tissues; concentrations of the stains and the staining schedule were not given. Recently, Waterman (1955) reported using a modified version of the Pianeze IIIb stain for rapid diagnosis of blister rust infection of white pine in preference to a slower stain schedule using orseillin and aniline blue.

Methods and Materials

Cubes or wedge-shaped pieces, ¼-inch on a side and including both bark and wood, were cut from typical rust galls. The pieces were boiled in water for at least 10 minutes to remove resin and air. No fixing solution was used. The pieces were then placed in distilled water for immediate sectioning or in a formalin-propionic acid-alcohol solution[1] for storage. Radial sections, including both bark and wood, were cut as thin as possible by hand, using a razor blade under a dissecting microscope. The sections were transferred to 70 percent alcohol for temporary storage or directly to the first stain.

Of the several stain combinations tried, including the revised Pianeze IIIb (Waterman, 1955), two have proved most satisfactory. These are orseillin-BB and aniline blue, and safranin-O and aniline blue. The dye solutions used were 1.0 g. orseillin-BB in 100 ml. 3 per cent aqueous acetic acid; 0.5 g. safranin-O in 100 ml. of 50 percent alcohol (Colley, 1917); and

[1]Thirty-seven percent formalin, 5 ml.; propionic acid, 5 ml.; 70 percent alcohol, 90 ml.

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0.25 g. aniline blue in 00 ml. of 90 percent alcohol. Solutions were applied by pipettes to the sections in Syracuse watch glasses and were drawn off by absorbent paper. Staining directly on the slides was possible, but troublesome.

Stain schedule is as follows:

1. Stain in orseillin or safranin solution for 30 to 60 seconds.
2. Draw off excess stain solution.
3. Flood with 95 percent alcohol (containing 0.5 g. picric acid crystals per 100 ml. if safranin was used).
4. Draw off alcohol.
5. Stain in aniline blue solution for 15 to 30 seconds.
6. Draw off excess stain solution.
7. Flood with 95 percent alcohol, slightly acidified with hydrochloric acid (Johansen, 1940), for 15 to 30 seconds.
8. Flood with absolute alcohol for 30 seconds.
9. Transfer to clove oil and examine.

If permanent mounts are desired:

10. Leave in clove oil as needed to clear.
11. Rinse in xylol for 30 minutes or longer.
12. Mount in balsam.

Results

The methods described have been used successfully for distinguishing the mycelium of *Cronartium fusiforme* in hand sections of slash and loblolly pines and for *C. cerebrum* in shortleaf pine.

Cronartium fusiforme and *C. cerebrum* have similar mycelial characteristics. Their hyphae are intercellular with characteristic haustoria penetrating the host cells. In radial section, the hyphae appear to separate the ray parenchyma cells of the bark and wood and abundant haustoria are found penetrating the host cells (Fig. 1). The haustoria appear constricted where they pass through the cell walls and then increase in size up to three times the width of the parent hyphal strand. They may or

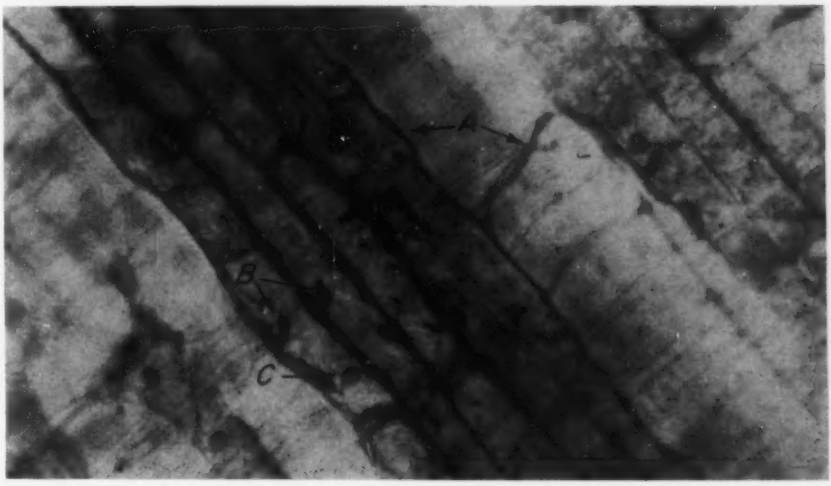

FIGURE 1. *Photomicrograph (325×) of a hand section of slash pine infected by* Cronartium fusiforme *and stained by orseillin and aniline blue: A, Intercellular hyphae; B, haustoria; and C, host cell nucleus.*

may not be closely associated with the host-cell nuclei. As yet, no haustorial branching has been observed, as reported for *C. ribicola* (Colley, 1917).

A well-stained slide using orseillin or safranin and aniline blue had the ray and bark cell walls dark blue, the cell nuclei a bright red, and the cell cytoplasm a faint red to a light reddish blue. When orseillin was used the resin duct parenchyma cells stained a deep red and the tracheid walls a faint pink or took no stain, but with safranin the resulting colors were blue and red, respectively. The hyphae of the parasite stained blue for the most part, usually a lighter blue than the host cell walls. The haustoria, especially the older ones, stained a darker blue than the hyphae, and were in strong contrast to the lighter stained host cells. The color differences plus the intercellular position of the mycelium and the presence of haustoria clearly distinguished the parasite from the host.

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Estimating Surface Area of Ponderosa Pine Foliage in Central Arizona

BY
DWIGHT R. CABLE

A MEASURE of the quantity or surface area of foliage of forest trees is useful to foresters, ecologists, and plant physiologists who study such problems as interception of precipitation, light transmission through forest canopies, rate of deposition and decay of forest litter, and effect of canopy on evaporation from the ground.

Methods

Equations developed for estimating surface area of foliage of ponderosa pine (*Pinus ponderosa* Laws.) are based on data collected at the Sierra Ancha Experimental Forest in central Arizona. These equations were derived by the method of least squares. In developing the equations for estimating surface area of foliage, surface area was related to weight of needle fascicles because foliage or fascicle weight is easier to measure than foliage area.

The individual needle fascicle is the basic unit of foliage used to determine the surface area of foliage on a pine tree. A ponderosa pine fascicle consists of a cluster of 3 needles, or occasionally 2 needles, with a persistent basal sheath. The needles form a cylinder. In cross section, each needle has 2 flat radial faces and 1 curved outer face representing one-third of the circumference of a circle.

Relationship of Foliage Weight to Tree Diameter

Kittredge (1944) has shown that when tree diameter and weight of foliage are both expressed in logarithms, a linear relationship exists between foliage weight and tree diameter. By using measurements of tree diameter and foliage weight from 31 ponderosa pine trees in California, Kittredge developed the following equation for estimating weight of ponderosa pine foliage:

$$(1)\quad \log W = 1.67 \log D - 0.73$$

W, foliage weight, is measured in kilograms, and D, diameter, in inches.

From a comparison of estimating equations developed for 10 species and 28 stands representing a wide variety of locations, sites, and ages, Kittredge concluded that "the relation between leaf weight and diameter is applicable to trees of different sizes, densities, crown classes, and ages at least up to the culmination of growth and beyond that age for tolerant species in all-aged stands."

As a check on the applicability of Kittredge's equation to the Southwest, the foliage of 20 ponderosa pine trees varying from 1 to 20 inches d.b.h. was stripped, ovendried, and weighed. These trees grew in an uneven-aged, old-growth stand con-

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sisting primarily of ponderosa pine, with scattered Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and Gambel oak (*Quercus gambelii* Nutt.). Age of ponderosa pine varied from 26 to 110 years, and height from 7 to 88 feet. The forest stand is located at an elevation of about 6,700 feet; at this location, average annual precipitation is 32 inches. Approximately one-third of this precipitation comes during the summer, June through September; and two-thirds during the winter, October through May.

Classified by the age-and-vigor classification developed by Thomson for use with ponderosa pine in the Southwest, as presented by Pearson (1950), 14 of the 20 trees are in Age Class I (young blackjacks, mainly below 12 inches d.b.h.), 4 in Age Class II (sawtimber-size blackjacks), and 2 in Age Class III (young yellow pine). The 20 trees fall in Vigor Classes A and B (crowns 35 to 70 percent of tree height). Thus, no wolf trees, suppressed trees, or overmature yellow pines were included in the sample.

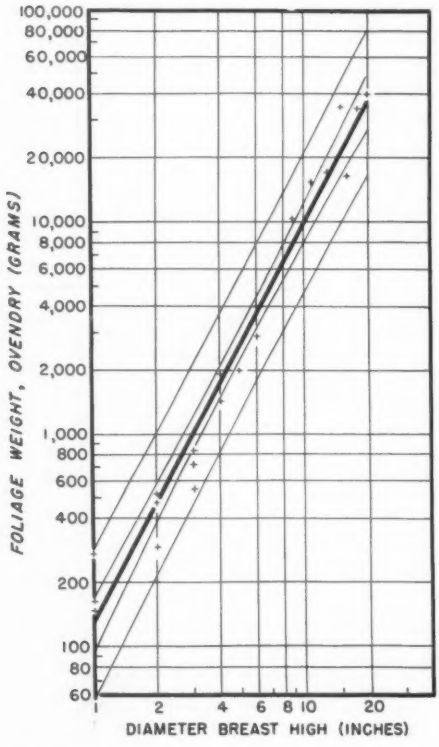

FIGURE 1. *Regression of foliage weight (ovendry) on tree diameter (d.b.h.), and 95-percent confidence bands for mean foliage weight of population (narrow band) and of individual tree (wide band) of given diameter.*

All fascicles on these trees were collected (excluding the current year's growth, which was just beginning at the time of collection—June and July). The fascicles were put in burlap sacks and left to air-dry for 2 or 3 months. Then they were oven-dried at 85° C. for 24 hours and weighed.

The equation developed for estimating weight of foliage for ponderosa pine trees of varying diameter is:

(2) $\log W = 1.8811 \log D - 0.8882$

W, foliage weight, is measured in kilograms, and D, diameter, in inches.

Throughout the range of the sample data, a 1-percent increase in tree diameter is accompanied by a 1.88-percent increase in foliage weight. The standard error of estimate for this equation is 0.1511 in logarithmic units. This equation is not much different from equation 1 developed by Kittredge.

Within the range of size, density, crown class, and age represented by the 20 sample trees, the data confirm Kittredge's conclusion quoted above.

Figure 1 illustrates the foliage weight-diameter relation. The narrow confidence band indicates the limits within which the mean foliage weight for the population of trees at a given diameter will lie, with a probability of 95 percent; the wide band indicates the 95-percent limits for any individual tree.

Relationship of Fascicle Area to Weight

The relation between fascicle area and weight is needed to convert foliage weight

to surface area. For this calculation, 100 individual needle fascicles were collected from trees of varying diameter, in a random manner, from all parts of the crowns. Total surface area of each fascicle (consisting of the 6 radial faces plus the external surface) was determined from the length and average diameter, by the method developed by Kozlowski and Schumacher (1943). Ovendry weights of the 100 fascicles varied from 0.0685 to 0.3428 grams (dried at 85° C. for 24 hours). Length of fascicles varied from 98 to 200 millimeters. Surface area varied from 7.875 to 23.968 square centimeters.

Fascicle area can be computed by the following equation:

$$(3)\quad FA = 5.645 + 54.502\ FW$$

FA, fascicle area, is measured in square centimeters, and *FW*, ovendry fascicle weight in grams.

According to this equation, fascicle area will increase 5.4502 square centimeters with each increase of 0.1 gram in ovendry weight. The standard error of estimate for this equation is 1.0384 square centimeters.

Figure 2 shows the relation between fascicle area and weight. The two confidence bands indicate the 95-percent limits for estimates of fascicle area for the population mean (narrow band) and for individuals (wide band) at any fascicle weight.

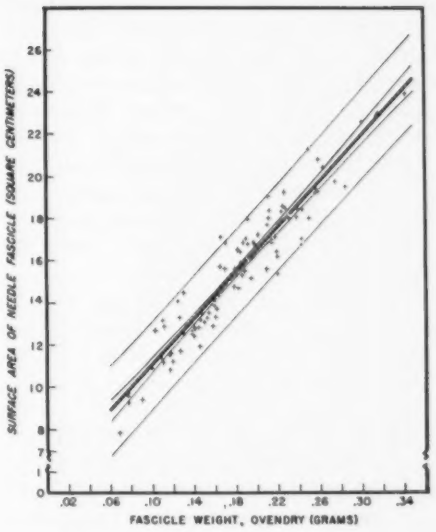

FIGURE 2. *Regression of fascicle surface area on fascicle weight (ovendry), and 95-percent confidence bands for mean area of population of fascicles (narrow band) and for area of individual fascicle (wide band) for fascicles of given weight.*

Relation of Average Needle Cluster Weight to Tree Diameter

The fascicle area per tree can be determined from equation 3 when the average fascicle weight and the total number of fascicles are known.

The best method of obtaining the weight of the average fascicle on a tree is to pick and count all the fascicles on the tree, ovendry and weigh them, and divide the weight by the number of fascicles. This is not too difficult with small trees, but with large trees some form of sampling must be used.

For this purpose, samples composed of 100 fascicles each were collected from each of 11 trees ranging from 1 to 18 inches d.b.h. The number of samples taken varied from 31 from a 1-inch d.b.h. tree (essentially a 100-percent sample) to 100 samples (10,000 fascicles) from each of the trees larger than about 5 inches d.b.h.

In collecting the fascicles, branchlets were gathered from all parts of the tree crowns, and all fascicles on the branchlets collected were included in the sample. In this way the samples contained fascicles of all ages and sizes growing under the entire range of conditions with respect to position on the crown and exposure to light.

These samples were ovendried at 85° C. for 24 hours and weighed in grams. The mean of the samples from each tree when divided by 100 (number of fascicles in each sample) was taken as the weight of the average fascicle on the tree.

To determine whether the variations in mean fascicle weights among the 11 trees

bore any relation to the size of the tree from which the fascicles came, a linear regression analysis was made. Mean ovendry weight per fascicle was used as the dependent (y) variable and diameter breast high as the independent (x) variable. The relation proved to be highly significant ($r = 0.825$), showing that larger trees tend to have larger and heavier fascicles. The equation for estimating mean weight per fascicle from tree diameter is:

(4) $MWF = 0.00514\ D + 0.1111$

The standard error of estimate for this equation is 0.0207 gram. MWF, mean weight per fascicle, is measured in grams and D, diameter in inches.

Figure 3 shows the relation between mean fascicle weight and tree diameter. The two 95-percent confidence bands indicate the limits of the range of population mean fascicle weight and individual tree mean fascicle weight for any given tree diameter.

The relation between mean fascicle weight and tree diameter applies most specifically to the uneven-aged, fully stocked stand from which the samples were taken. Because variable light conditions affect leaf development differently, another relation may hold for other stands.

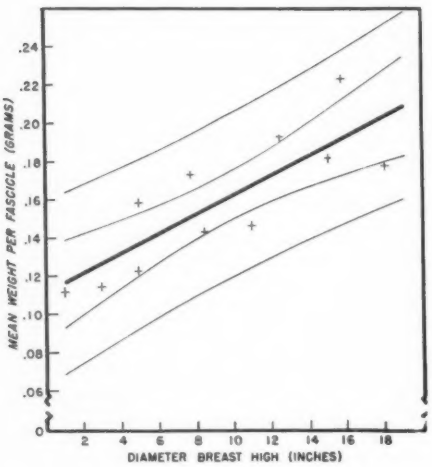

FIGURE 3. *Regression of mean ovendry weight per fascicle on tree diameter, and 95-percent confidence bands for mean fascicle weight for the population of trees of a given diameter (narrow band) and for an individual tree (wide band).*

Estimating Surface of a Tree's Foliage

To estimate the surface area of foliage of a tree, calculate the total weight of foliage (equation 2), divide by mean weight per fascicle (equation 4), and multiply by surface area of the average fascicle (equation 3).

As an example of the procedure: from equation 2 the ovendry weight of foliage on a 6-inch tree should be 3,764 grams. From equation 4 the mean ovendry weight per fascicle on a 6-inch ponderosa pine is 0.1420 gram. Dividing 3,764 by 0.1420 gives an estimated 26,507 fascicles. From equation 3 the estimated surface area of a fascicle weighing 0.1420 gram is 13.38 square centimeters. Multiplying the estimated total number of fascicles by the estimated surface area per fascicle gives an estimated 35.5 square meters of surface area of foliage on the 6-inch tree.

Estimating Surface Area from Tree Diameter

Using equations 2, 3, and 4 as described above to estimate foliage surface area for each diameter class yields the regression shown in Figure 4. This expression of foliage surface area as a function of tree diameter can be used to estimate total foliage surface area for ponderosa pine trees of varying diameter growing in fully stocked, uneven-aged stands. No error of estimate can be determined for this relation since the surface area values are estimates from regressions and not actual measurements.

Total surface area of foliage for a fully stocked, uneven-aged ponderosa pine stand with crown-class structure similiar to that of the sample trees can be estimated from a stand table by accumulating the foliage surface areas of the trees comprising the stand as determined from Figure 4.

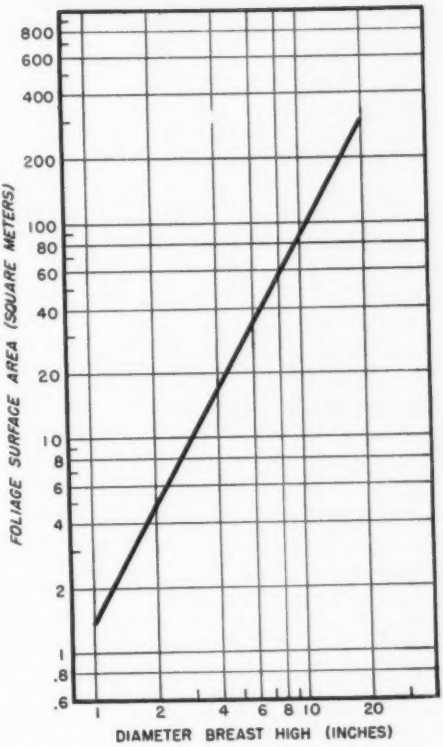

FIGURE 4. *Regression of foliage surface area on tree diameter.*

Summary

Regression analyses that show the relationship between surface area and ovendry weight of individual ponderosa pine fascicles are presented for ponderosa pine in Arizona. By use of equations developed by the method of least squares, surface area in square centimeters can be estimated from needle weight.

The relationship between surface area and weight of the individual fascicle is used, together with an estimate of the total number of fascicles on a tree, as a basis for computing the total surface area of foliage on entire trees.

Estimates of total number of fascicles on a tree are derived from the relationship between total weight of foliage and tree diameter on entire trees, and from the relationship between weight of the average fascicle and tree diameter.

Surface area of foliage on an acreage basis can be determined by accumulating the foliage surface areas of the individual trees comprising the stand.

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Tetrazolium Chloride to Test Loblolly Pine Seed Viability

BY
CHARLES X. GRANO

CONVENTIONAL METHODS of testing the viability of pine seed have several drawbacks, chief of which is the long time often required to complete the tests. Other shortcomings are large space requirements; also the possibility of inaccurate results where fungus infections, seed dormancy, or variations in the temperature of the testing room are encountered. In search of techniques free of these failings many approaches have been tried, most of them being attempts to measure physiological responses to various treatments (Waller, 1901; Flemion, 1948; Gadd, 1950).

One of the most promising of these techniques is biochemical and makes use of 2,3,5-triphenyltetrazolium chloride. It is based on the action of reducing enzymes, classed as dehydrogenases, which are found only in living tissue. This chemical is a non-poisonous, colorless salt that is reduced to a carmine-red formazan in the presence of dehydrogenases. It is generally held that only living embryos are colored red when immersed in a solution of the salt, though Brown (1954) states that the tetrazolium test is not exact because oils present in most plant embryos, even after death, can be stained under certain conditions. Smith (1951) has made an extensive review of the literature on tetrazolium salt with respect to its reduction by enzymes in living matter and the staining of plant tissue.

Tetrazolium bromide, a chemical similar to tetrazolium chloride, has given satisfactory results in England on various species (Holmes, 1949, 1950, 1951). Tetrazolium chloride has been tried to a limited extent in the United States (Flemion and Poole, 1948; On, 1952). Recently, it was tested on loblolly pine (*Pinus taeda* L.) seed at the Crosset Research Center of the Southern Forest Experiment Station. The results agree closely with those from germination in sandflats.

Method

The seeds were soaked overnight in tap water, as there is evidence that this assists quick, clear staining.[1] After being soaked for about 12 hours, the seeds were cut in the longitudinal plane, slightly off center, so that the embryo was exposed at the cut surface of the larger portion of each seed. The smaller portion of each seed was discarded and the larger portion was immersed in a 1-percent solution of 2,3,5-triphenyltetrazolium chloride in distilled water. Fresh solution was prepared as required.

Because tetrazolium is light-sensitive, the solution was stored and seed embryos were treated in total darkness. Treatment consisted of storing immersed seeds in a light-

[1]Personal communication from G. D. Holmes, Forestry Comm. Gt. Brit., 1953.

The author is a Silviculturist, Southern Forest Experiment Station, Forest Service, U. S. Department of Agriculture.

tight container at room temperature (68° F.) for 24 hours.

After immersion the embryos were excised intact from the endosperm for examination under a stereoscopic microscope. As previously cut surfaces of the embryos did not stain well, the undamaged sides were used for classification.

Unless the stain is fixed, embryos must be examined within one hour after removal from the solution because of the danger of coloration of unstained specimens by photoreduction. Immersing the excised embryos in a 15-percent formalin solution for 15 minutes fixes the stain and makes possible accurate evaluation several days after staining. If the fixed embryos are grouped on a glass slide and covered with a mounting medium, they will keep for long periods. This permits evaluation whenever it is convenient. In commercial or other large-scale testing, permanent mounting on slides may be eliminated, as the embryos are usually discarded after examination.

In all but a very few cases, it was found that when staining did take place the entire embryo was colored. There was, however, a variation in the intensity of staining or depth of color among the embryos. Consequently, intensity of color was used to classify viable seeds as to probable ability to germinate. The percentage of deeply stained embryos was found to approach the sandflat germination figures most closely. The standard of comparison was an embryo whose depth of red stain approximated that listed as 5RP 4/12 in the Munsell Neighboring Hues Edition. Embryos equaling or exceeding this standard intensity of coloration were classed as deeply stained and therefore viable.

The results obtained by the chemical test were checked against standard sandflat germination trials conducted as recommended by Wakeley (1954).

The loblolly pine seed for this experiment was obtained from 10 seed lots varying in age and quality. Eight 100-seed samples from each of the 10 lots were tested in pairs, one member of each pair chemically and the other member by sandflat germination. In all, 4,000 seeds were tested by each method.

Results

Percent of seed showing deeply stained embryos is compared with sandflat germination percent in Table 1.

The correlation coefficient for germination percent of unstratified seed with percent of same seed lot showing deeply stained embryo was —.101, or far less than the .632 value of r required for significance at the .05 level with 8 degrees of freedom.

The lack of correlation seemed to be mainly due to the very poor germination of seed in lots 7, 8, and 9. Since these lots appeared from the chemical test to have the capacity for high germination, it was suspected that they were in a state of dormancy that could be broken only by a drastic measure such as cold moist stratification. Seed from these 3 lots was therefore stratified for 10 weeks at 40° F. in moist sand, and then another sandflat germination test

TABLE 1. Comparison of sandflat germination with chemical viability test.

Seed lot	Proportion of full seeds germinating in sandflats		Proportion of full seeds with deeply stained embryos[2]
	Unstratified	Stratified[1]	
	Percent	*Percent*	*Percent*
1	81.1	.....	91.7
2	50.0	.....	76.7
3	79.4	.....	92.1
4	35.3	.....	28.4
5	60.5	.....	56.8
6	46.7	.....	47.6
7	29.4	100.0	100.0
8	10.1	94.3	95.8
9	15.8	94.3	96.7
10	58.5	.....	66.7

[1]Stratification was in moist sand at 40° F. for 10 weeks; it was applied to 3 seed lots where dormancy of unstratified seed was indicated by a large difference between proportion deeply stained and proportion of unstratified seed germinating.

[2]Full seeds include those with an endosperm, with or without an embryo.

was run. It indicated that dormancy of these lots could be broken by stratification. When the germination percents for lots 7, 8, and 9 *after* stratification (Table 1) were substituted in the analysis, the correlation coefficient was +.918. This value greatly exceeded the .765 value of r required for significance at the .01 level with 8 degrees of freedom.

For the 10 lots tested (using stratification where indicated) the relationship between sandflat germination percent and percent with embryos deeply stained could be expressed as: Sandflat germination percent = 5.9 percent plus (.851 times percent stained), with a standard error of estimate equal to ± 9.5 percent.

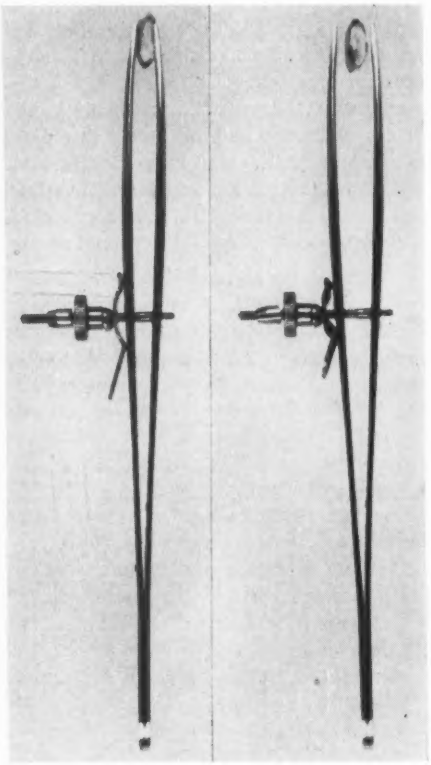

FIGURE 1. *Forceps modified to permit rapid closure and opening, and firm positioning of seed without fatiguing finger pressure.* LEFT: *Seed in position for excision.* RIGHT: *Seed is released by flipping release bar upward.*

Discussion

The outstanding advantage of the chemical method is its ability to provide reliable viability results on short notice—48 hours or less. This does not mean that the chemical method is faster than the sandflat method in terms of the number of seeds that can be treated per man-hour. In well-organized seed-testing establishments, about two or three times more seeds can be tested per man-hour with sandflats. As chemical testing comes into general use, however, better equipment and techniques will undoubtedly be developed.

For example, in this test conventional forceps were modified so as to speed up the work of excising embryos (Fig. 1). These modified forceps permitted rapid closure on seed, firm positioning of seed without fatiguing finger pressure, and quick release of seed parts after excision by simply flipping the release bar. The inside surfaces of the forceps tips were hollowed slightly to conform roughly to seed shape.

Instead of using the mountants usually employed in microscopy, the author applied a rapidly drying clear acrylic spray from an aerosol bomb dispenser. After the embryos had been arranged on a microscope slide following the formalin bath, they were permitted to dry for 10 minutes and then covered with a light film of the spray. This method is very rapid, and fixes the embryo to the slide with a glass-clear, air-tight film. One year after mounting, no color deterioration of the stained embryos has been noted. The spray is sold under the commercial name Krylon acrylic spray No. 1301.

In their present state the chemical viability methods do not provide a measure of germinative vigor. Although sandflat tests leave something to be desired in this respect, they do provide data on rapidity of

germination, shape of cumulative germination curve, and percentage and nature of abnormal germinations — all of which are useful indicators of germinative vigor.

The chemical method provides a reliable measure of potential germinative capacity, independent of seed dormancy. By the same token, however, it does not reveal the need for stratification.

All other advantages claimed for the chemical method stand without qualification.

Summary

The viability of 10 lots of loblolly pine seed of varying age and quality was determined by immersing wet seed in a 1-percent aqueous solution of 2,3,5-triphenyltetrazolium chloride. Viability percent based only on those seeds which were deeply stained by this treatment closely agreed with sandflat germination checks.

A modified forceps which facilitated embryo excision, and the use of an acrylic spray for permanent mounting of embryos on slides, are described.

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Comments on Some German and Swedish Thinning Experiments in Norway Spruce

BY
ERIK HOLMSGAARD

ASSMANN'S THEORY that the volume increment depends on stand basal area has been the subject of much attention in forestry literature in recent years. The gist of this theory is that the greatest volume increment is obtained in stands with a so-called "optimal basal area," and that the increment is smaller for stands having basal areas that are either larger or smaller. Furthermore, Assmann[1] is of the opinion that the optimal basal area varies in different localities. For Norway spruce (*Picea abies* (L.) Karst.) it is highest in areas where growth is good.

In addition to the maximum basal area (the largest basal area obtainable in a given locality) and the optimal basal area, Assmann introduces a third concept: the critical basal area. This he defines as the basal area in which the volume increment is proved to have been reduced by at least 5 percent in relation to the volume increment obtained at the optimal basal area.

Experiments in Germany

Assmann (1954) published a paper on 6 series of thinning experiments which seems to bear out the theory so far as Norway spruce is concerned, at any rate on the sites examined. These thinning experiments were established in 4 localities in Bavaria at altitudes between 1740 and 2720 feet. The annual precipitation ranges from 37 to 49 inches, 16 to 22 inches of which falls from May to August. The stands in question are of the quality classes 0.0 to 1.7 after Wiedemann (1936). The thinning experiments are of long standing and all stands are more than 80 years old. Each series of experiments comprises A, B and C thinnings. Assmann gives only the smoothed increment figures for the period between the ages of 50 and 80 years; the actual increment figures obtained not being included in the paper.

The 6 series of experiments show that the volume increment culminates in basal areas of between 222 and 335 sq. ft. per acre at ages between 50 and 80 years, the highest figures applying to the best quality classes (Table 1).

It will be seen that the critical basal area decreases from 261 to 200 sq. ft. when the quality decreases from 0 to 1.7. In any case, the critical basal area is found at about 75 percent of the maximum basal area.

The investigations are particularly interesting because they are based on data which originated from actual thinning experiments and not—as is the case with many other investigations of the influence

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of the thinning grade on the yield—from statistical treatment of observations from scattered single sample plots. Assmann's investigations must therefore bear considerable weight in the discussion as to whether it is justifiable to talk about optimal basal areas and about a basal area optimum for a locality.

Experiments in Sweden

At Halmstad in Southern Sweden the Swedish Forest Experiment Station has at its disposal the experimental forest of Tönnersjöheden, where 5 series of thinnings in Norway spruce exist. The results of these experiments have been reported on by Carbonnier (1954).

The annual precipitation in this region is about 40 inches, 37 percent of which falls in the period May to August. The soil consists of sandy, stony moraine and the ground is rather hilly. The Norway spruce stands in question are of the quality class 1–2, Wiedemann, (1936).

The thinning experiments were established in spruce stands planted between 1878 and 1891 following harvest of beech. The oldest of these experiments was established in 1906, the 4 others in the years 1911, 1924, 1925 and 1927. All series of experiments have been measured for at least 25 years. None of the stands had been thinned before the establishment of the experiments.

While the German experiments used by Assmann in his analysis are *thinning grade experiments*, the experiments in Sweden are primarily *thinning method experiments*, the latter being rather schematic as follows:

1. *No thinning (5 plots.)*
2. *Thinning from below.* In the first thinnings the diameter of the trees thinned was 50 to 60 percent of the diameter of the stands held over; in the last thinnings it was 80 to 90 percent (eventually, no small trees were left at all). All together, there are 7 plots, 5 of which must be characterized as heavily thinned, 2 as extra-heavily thinned.
3. *Crown thinning,* in which the thinning was made primarily among the dominant and codominant trees, part of the non-dominant trees being arbitrarily held over. At first, the diameter of the trees thinned was 80 to 90 percent of that of the trees retained; later it dropped to 70 percent or below. All together, there are 6 plots, 5 heavily thinned and 1 extra-heavily thinned.

In establishing thinning experiments it is always difficult to insure that the selected plots have perfectly uniform growing conditions, and considering the uneven ground of the region in question, it seems to be particularly difficult to establish applicable thinning experiments there. Even so, Carbonnier's investigations clearly show that the quality does not vary appreciably within the individual experimental series. The variations, however, are so great that some details on which it would have been interesting to have had information, cannot be explained on the basis of this, otherwise very extensive, material. But since the 5 series support each other on essential points it is possible to draw several interesting

TABLE 1. Basal-area levels in the interval of 50-80 years.

Series of experiments		Site class (After Wiedemann)	Average stem volume increment, 0–80 years	Approximate basal area level		
				Maximum	Optimal	Critical
			Cu. ft. per acre		*Sq. ft. per acre*	
Ottobeuren	8	0.0	290	348	335	261
Sachsenried	2	0.5	279	327	287	240
Sachsenried	3	0.7	243	327 (?)	283	240
Denklingen	5	0.8	224	279	248	218
Eglharting	72	1.7	180	253	231	200
Eglharting	73	1.6	176	253	222	200

conclusions from the experiments.

Between the ages of 60 and 70 years, the unthinned plots had basal areas that ranged from 218 to 261 sq. ft. per acre; after thinning the thinned plots had basal areas of 100 to 148 sq. ft. per acre.

The current volume increment (stem volume above stump height) has been increasing constantly since the establishment of the experiments and has not yet culminated at an age of about 75 years, while, according to yield tables, the culmination occurs at an age of about 40 years.

In all 5 series, the crown thinning has resulted in a somewhat smaller increment in the past 25 to 30 years than the thinning from below. On an average, the difference amounts to some 5 percent. One of the effects of the crown thinning should be to favor the development of the smaller trees. The experiments show, however, that the crown thinning has given only a slight stimulus to the trees which were not dominant or codominant.

Since the start of the experiments the increment of the untreated plots has averaged 98 percent of that of the plots heavily thinned from below. However, the untreated plots contain somewhat more birch than the plots heavily thinned from below, and since Carbonnier has found that the yield is reduced adjacent to the birches, he assumes that there would not have been any difference if the stands had been perfectly pure.

The financial yield value has been calculated for the individual sample plots. Taper has been calculated on the basis of the same tables for all thinning methods, with entries for height and diameter for all trees. In the untreated plots the net yield has amounted to only 70 to 80 percent of the yield in the thinned plots, Carbonnier not having included any value for the volume falling to the ground in the uncut plots (although this volume is included in all increment figures). No distinct difference between the net yields and capitalized value (i.e. the value of all yields referred to the same point of time) of the two thinning methods can be deduced from the material, although their are indications that crown thinning is a little inferior to thinning from below.

These experiments in Sweden treat the thinning problems on the basis of direct observations of the course of increment, with no adjustment whatever of the tree measurement figures. All the results of measurements have been given, enabling the reader to form his own judgment of the reliability of the conclusions.

Discussion of German, Swedish and Other Results

It might be interesting to see how Carbonnier's quite extensive material compares with Assmann's points of view. Unfortunately, however, the Swedish material is not very suitable for the purpose, since the thinning grade is almost the same in most of the thinned plots. Thus, there are no very light thinnings which according to Assmann's investigations give the maximum increment on good spruce sites (high in rainfall).

The 3 plots which are characterized as "extra heavily" thinned (1 crown thinning and 2 thinnings from below) are, however, of some interest in this connection. They have basal areas of 122, 100 and 118 sq. ft. per acre, respectively, (ave. 113 sq. ft.) after thinning at the age of 60 to 70 years. Compared with the "heavily" thinned plots with thinnings of the same type (with basal areas of 135, 118 and 144 sq. ft. per acre (ave. 131 sq. ft.) the "extra heavily" thinned plots have:

1. Smaller increment. The total volume increment has been 3, 4 and 10 percent (ave. 6 percent) less.
2. A net yield value which has been 13 percent higher, 1 percent lower and 9 percent lower (ave. 1 percent higher).
3. Capitalized values at a rate of interest of 3 percent are 19 percent higher, 1 percent higher and 5 percent lower, respectively (ave. 5 percent higher).

It might look as if a thinning ending in a basal area of 113 sq. ft. per acre instead of 131 sq. ft. at 60 to 70 years, results in a loss in the total volume increment of about 6 percent. This value is, however, inaccurate because of unequal stand heights at the time treatment started. When account is taken of the differences in site class it is found that the loss in total volume increment should be reduced to about 3 percent, a figure, however, which is still most uncertain.

The 3 "extra heavily" thinned plots have actually yielded a stem volume 6 percent less than that of the plots with which they were compared; let it then be assumed that this is due to the heavier thinning rather than accidental differences in soil, etc. On account of the larger dimensions obtained, the net value of the yield volume has, nevertheless, been just as high as in the plots which were only "heavily" thinned, and if compound interest calculation is applied, the extra heavy thinning has an obvious advantage.

Thus, the Swedish thinning experiments illustrate that the increase of the thinning grade to a basal area after thinning of about 50 percent of the maximum basal area may be of financial advantage, although involving an increment loss of the order of 6 percent.

The efforts being made to ascertain whether or not optimal basal areas exist, should be followed attentively. As will appear from the Swedish investigations, there is no reason to believe that the most advantageous silvicultural treatment, from an economic or a financial point of view, is just the one giving the largest volume increment.

The question of what thinning grade is most advantageous has been the subject of discussion as long as any living forester can remember, and many are no doubt of the opinion that no headway is being made. Undoubtedly, it must be admitted that little is yet known about the influence of the thinning grade on the increment. The increment may be assumed to be constant within a rather wide interval, as Möller does, most recently in a paper on thinnings in Denmark published in English (Møller, 1954). This is in conformity with the universally recognized scientific principle that no action may be ascribed any effect until it has been proved with some certainty that there actually is an effect. In his comparison of experimental results, Møller assumes that the effect of thinning will be the same in all localities. Whether this assumption is correct must, for the present, be considered a matter of opinion; but there is a possibility it may be wrong.

There is, however, no denying that most of the hitherto published papers showing that the increment is dependent on the thinning grade are open to serious objections.

These objections may have relation to:

1. Insufficient analysis of the material.
2. Insufficient information about the basic material, for which reason the reliability of the analysis cannot be assessed.
3. The thinning experiments have been underway for too short a time.

The last point, viz. the time element, has possibly been given too little attention. On this point the experiments described by Carbonnier may throw some light.

In four of the experimental series the untreated plots have been measured from the start of the experiment. In these cases the volume increment of the thinned plots may be expressed in percentages of the volume increment of the untreated plots, so that the effect of the thinning on the long-range course of the increment may be known. This is a question which Carbonnier himself has not discussed, but the requisite values can be deduced from his Table 1, as shown here in Figures 1 and 2. From the figures it appears that, immediately after the initial thinning the volume increment of the thinned plots was considerably greater than that of the untreated plots (in which, however, there was a somewhat larger mixture of birch), but that the increment gradually falls, ending

well below the increment of the untreated plots.

The drop in the relative increment of the thinned plots must be assumed to be a reality, since the 4 series of experiments in which comparison is possible all show the same result. One-sided errors in d.b.h. measurement must be ruled out of consideration because in all revisions the basal area determination has been based on crosswise calipering of all trees.

The high volume-increment level shown in the figures immediately after the initial thinning may be due partially to the fact that the thinned plots are of a better site quality class than the untreated plots. For the plots thinned from below and shown in Figure 1, the volume at the beginning of the experiments amounted to 103, 109, 103 and 104 percent (ave. 105 percent) of the stand on the untreated plots; for the crown-thinned plots the percentages are 105, 117 and 110 (ave. 111). But even if these figures are taken as expressions of a real quality-class difference, the increment in the first cutting cycles nevertheless seems to be relatively higher in the thinned plots than in the untreated plots.

As far as the author knows, the sample plots in Southern Sweden are the first fairly reliable examples of thinning having provided a stimulus to the volume increment per acre, and of this stimulus gradually ceasing and being followed by a reduced increment. As an explanation of this fact, it might be most natural to assume, as does Romell (1938), that the thinning brings about a liberation of nutrients through decomposition of roots of the felled trees and other modifications of the soil. When these effects wear off the increment drops again.

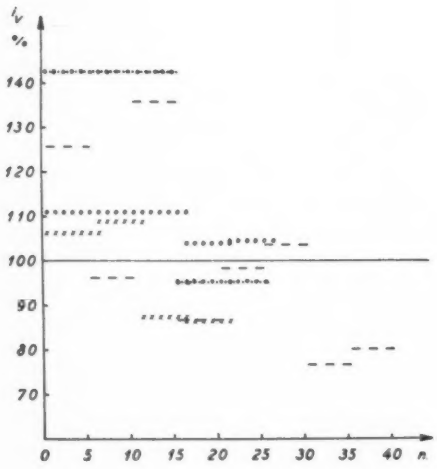

FIGURE 1. *Ordinate: The volume increment in plots heavily thinned from below, expressed in percentages of the increment in the untreated plots, each experimental series having a symbol of its own. Abscissa: Number of years since initial thinning took place. (After Carbonnier, 1954).*

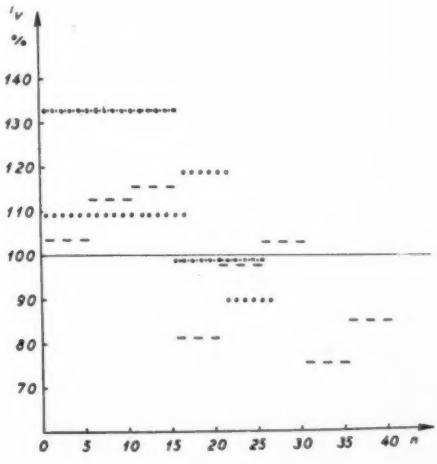

FIGURE 2. *Ordinate: The volume increment in heavily crown-thinned plots, expressed in percentages of the increment in the untreated plots, each experimental series having a symbol of its own. Abscissa: Number of years since initial thinning took place. (After Carbonnier, 1954).*

In the last remeasurements the increment for the thinned plots has decreased to values below those of the increment for the unthinned plots. This may be because the liberation of nutrients is now smallest in the thinned plots. It may, however, be more natural to assume that the denser the stand or the larger the basal area in a locality of high rainfall, the greater the increment will be—*all other conditions being equal* (in Assmann's terms: the optimal basal area is high). In the most recent examinations, the liberation of nutrients may have been the same in the untreated plots and in the thinned plots, and the unthinned ones may therefore have had the highest increment. After the initial thinnings the effect of the greater density in the untreated plots was less than the increment-stimulating effect of the liberation of nutrients in the thinned plots.

If the results of Norway spruce experiments in Sweden prove to have a more widespread applicability, caution, in regard to the effect of the thinning grade on the volume increment, should be exercised in drawing conclusions from experiments which do not comprise the whole rotation. The experimental series underlying Assmann's investigations were not so accurately measured in the younger ages, and so Assmann has presented data only for the period from 50 to 80 years. If the effect of the thinning grade on the volume increment in South Germany is dependent on age in the same way as appears from the Swedish experiments, this means that Assmann's investigations must give a one-sided picture of the influence of the thinning grade on the volume increment—a picture in which the light thinning grades take up too favorable a position. Unfortunately, there are so few old thinning experiments in the world that sufficient material for thorough testing the universal validity of the Swedish experiments is not believed to be available.

Reference may, however, be made to Burger (1951), who is of the opinion that the thinning grade has but little effect on the volume increment of Norway spruce, and who published increment figures from a thinning experiment at Olten as the only support for this belief. The experiment, which comprises B, C and D thinnings, was established in 22-year-old spruce and has been measured over 62 years. In the measuring period the B-thinning (in which all dry and suppressed spruces were removed) has yielded 17,105 cu. ft. per acre, the C-thinning 16,919 cu. ft., and the D-thinning 17,062 cu. ft.,—practically the same yield irrespective of the thinning grade. Engler (1924), in a number of thinning experiments, found that, on an average, the heavy thinning grades gave the highest yields, and the sample plots at Olten mentioned by Burger were no exception, since in the period 22 to 54 years they had an average yearly total-volume growth of:

Thinning Grade	*Cu. Ft. per Acre*
B	289
C	312
D	320

According to Burger the sample plots have produced virtually the same volume in 84 years. It can then be concluded that in the last part of its lifetime there was as much more yield in the lightly thinned plot (as compared to the heavily thinned plot) as there was less yield during the first half of the observation period. This Swiss thinning experiment thus indicates that the long-range course of the volume yield in the Swedish thinning experiments (Figs. 1 and 2) can also be found in other places, and that extra caution is required in drawing conclusions as to magnitude of the yield from thinning experiments which have not been closely followed for a very long time.

The influence of the thinning grade on the height and the trend of the curve of current or periodic increment as shown above and by Holmsgaard (1956) is supported in a paper by Assmann (Allg. Forstzeitschrift, 1957, pp. 329-333 and 349-351) appearing after this article went to press. Assmann shows that in four series of thinning experiments in European beech the long

range trend of volume increment is the same as borne out by the Swedish spruce experiments: in the first years following the initial thinning, the thinned plots produced much more than the unthinned but later on they produced less.

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Anotomical Development of the Hopocotyl Of Douglas-Fir

BY
FRANK H. SMITH

HEAT INJURY is one of the most important factors affecting the establishment of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in logged or burned areas (Isaac, 1938). The gross symptoms of heat injury have been described (Hartley, 1918; Bates and Roeser, 1924; Isaac, 1938). Baker (1929) discussed briefly some of the anatomical features of the seedling that might affect sensitivity to heat. Development of the embryo and the structure and development of the apical meristems of the seedling have been adequately described (Allen, 1947 a, b). The mature embryos and young seedlings of other conifers have been described by numerous investigators, only a few of which are cited here. These investigators have emphasized the occurrence of "secretory cells" in the embryo, the origin and structure of the vascular tissue, and the transition region of the seedlings. The continued development of the seedling, including the maturation of the primary tissues and the development of secondary tissues during the first season of growth, has in general been disregarded or only briefly considered.

This investigation includes the development of tissues in the hypocotyl from the mature embryo through to the end of the first season's growth. The primary emphasis is on the cells that are external to the vascular tissues, and especially on developments that might be responsible for the increasing resistance to heat injury as the seedling becomes older. Only normal development is considered here, but later investigations will attempt to correlate anatomical development with resistance to heat injury at various stages during this first year.

Material and Methods

Seed were collected[1] from west of the Cascade Mountains near Ashford, Washington, in the Snoqualmie National Forest at approximately 600 feet elevation and from east of the Cascades near Bear Springs, Oregon, in the Mt. Hood National Forest at an elevation of approximately 3,000 feet. The seed were germinated about April 15, 1956, and the seedlings were grown in the greenhouse until June 7, when they were moved outdoors. Embryos were obtained from stratified seed, and some of the youngest seedlings were obtained from seed placed in a germination chamber. Collections of seedlings were made at weekly intervals during the early part of the growing season and later at intervals of 2 or 3 weeks. Randolph's modification of Nava-

[1]These seed were obtained from the U. S. Forest Service, Portland, Oregon.

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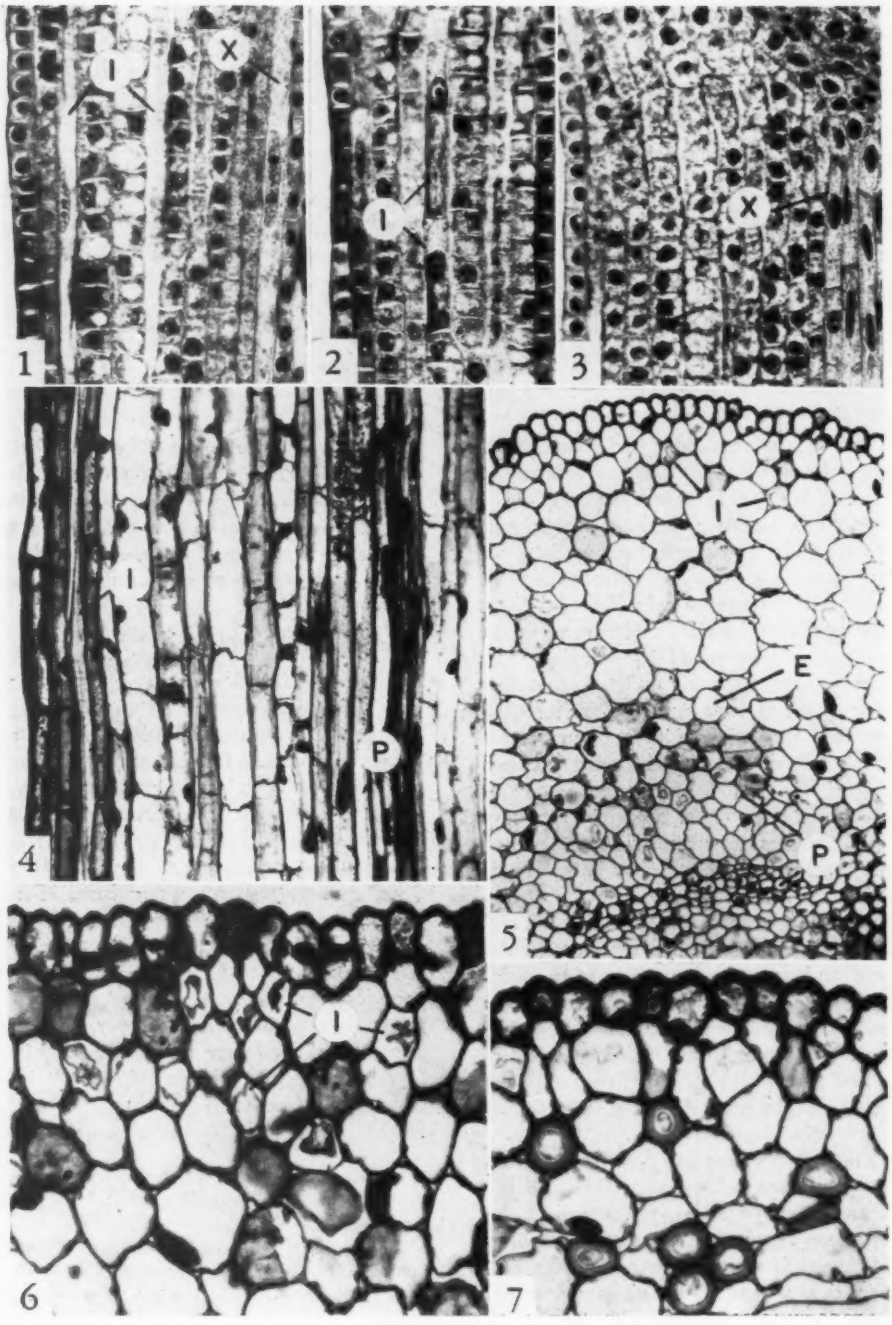
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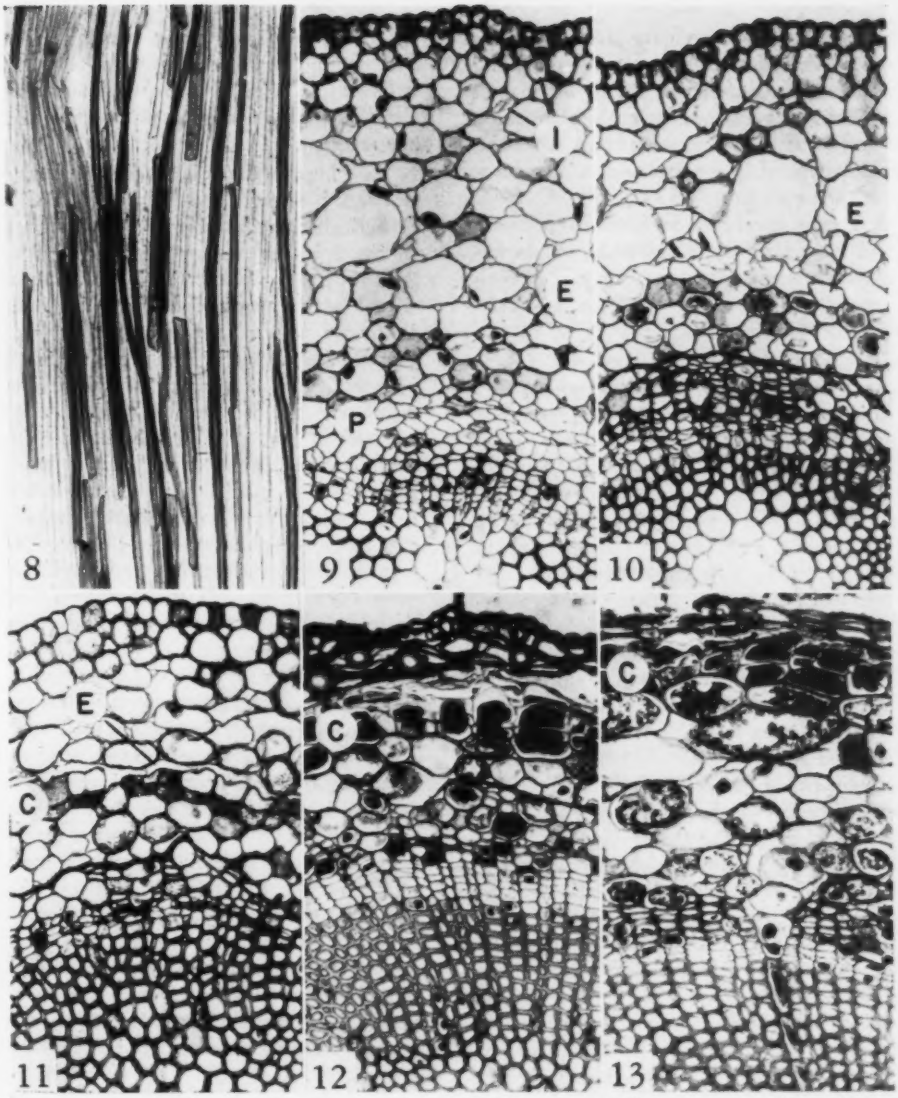

FIGURE 1. *Longitudinal section from mature embryo; I, sclereid initial; X, elongate phloem element.* FIGURES 2 and 3. *Longitudinal sections of embryo from stratified seed; I and X, sclereid initials and elongate phloem element that differentiated late in embryonic development.* FIGURE 4. *Longitudinal section of hypocotyl from seedling in loop stage; I, sclereid initial; P, phloem.* FIGURES 5 and 6. *Cross sections of 10-day old hypocotyl; E, endodermis; P, large outer cells and small inner cells of primary phloem.* FIGURE 7. *Mature sclereids in 6-week old hypocotyl. Figures 1-5,* $\times 200$; *6-7,* $\times$ *430.*

FIGURE 8. *Sclereids in cortex of hypocotyl at 6 weeks.* FIGURE 9. *Cross section of hypocotyl at 3 weeks.* FIGURE 10. *At 6 weeks.* FIGURE 11. *At 7 weeks.* FIGURE 12. *At 8 weeks.* FIGURE 13. *At 4 months. C, cork cambium; E, endodermis, I, sclereid initial. Figure 8,* $\times 100$. *Figures 9-13,* $\times 200$.

shin's killing solution gave the best results for all stages in development, but no killing solution gave satisfactory results for regions which were undergoing rapid elongation. Paraffin embedded material was soaked in a solution of glycerine and a detergent (Alcorn and Ark, 1953) at 38° C. for 2 to 7 days, sectioned at 8 to 10 microns, and stained progressively with iron hematoxylin and safranin.

Observations

The two seed samples were not significantly different with regard to tissue differentiation, with the possible exception of sclerenchyma in the cortex, so are not distinguished in the description of seedling development. Also, the rate of tissue differentiation in both groups of seedlings was so variable that actual age of the seedling was not particularly significant. Hence, the age indicated for any given stage of differentiation is only approximate and might not apply to an individual seedling.

The development of the embryo of Douglas-fir has recently been described in detail by Allen (1947 a) and will not be repeated here. Greatly elongated cells are prominent in the embryonic cortex and outer portion of the vascular region in the hypocotyl portion of the embryo of Douglas-fir (Fig. 1) and many other conifers. These cells have large nuclei, little or none of the reserve food materials that fill other cells of the embryo, and may extend almost the full length of the hypocotyl. Allen (1947 a), Schopf (1943), Spurr (1950), and many other investigators since Chaveaud (1903), have referred to these as "secretory cells." This designation appears to be a misnomer when applied to the elongate cells in the cortex of the hypocotyl of Douglas-fir. In this species these cells, as well as similar ones differentiated during the growth of the seedling, are initials that will mature as sclereids (Figs. 7 and 8), and hence should be termed sclereid primordia or idioblasts. The elongate cells at the outer periphery of the vascular region do not mature as sclereids but become crushed in the early stages of seedling development. Both of these types of elongated cells will be described in more detail in the description and discussion of the growth of the seedling.

The hypocotyl of the conifer embryo is developed almost entirely by intercalary growth during and after the establishment of the apical meristems (Allen, 1947 a; Schopf, 1943; Spurr, 1949). The abundant food reserves in the embryo of Douglas-fir are digested rapidly as the seed germinates and disappear first from the lower hypocotyl. Some intercalary cell divisions occur with the first growth of the embryo but cell enlargement in the lower hypocotyl is the primary factor in the emergence of the radicle. Either one or both cells resulting from some of the transverse cell divisions in the cortex may enlarge immediately and differentiate as sclereid primordia (Fig. 2). As the hypocotyl continues to lengthen mitotic activity increases, especially in the upper portion. Before the seedling reaches the loop stage, a broad intercalary meristem is established through the upper hypocotyl just below the cotyledonary node. There are numerous transverse divisions in the cortex and both transverse and longitudinal divisions in the procambium strands which lead to the cotyledons. Divisions in this intercalary meristem may also result in the differentiation of new sclereid primordia in the cortex and of initials in the outer procambium (Fig. 3) that will mature into greatly elongated cells similar to but shorter than those present in the dormant, mature embryo. The sclereid primordia are scattered throughout the cortex and are early distinguished from the other cortical cells. They develop more cytoplasm, enlarged nuclei, and do not undergo additional divisions but elongate rapidly. As Spurr (1950) demonstrated for pine, the extent of elongation of these cells is directly proportional to the extent of elongation of the region of the embryo in which they occur. Hence, the sclereid primordia which are differentiated early will become extremely long, fre-

quently 2 to 4 mm., while the ones differentiated by the later cell divisions in a given region will result in much shorter sclereids (Fig. 8). The same applies to the elongate elements, commonly termed "secretory cells," in the outer procambium.

The following description of the growth and differentiation of the hypocotyl applies only to the lower hypocotyl since this is the first portion to mature and is also the region where heat injury is usually localized. The upper portion develops in a similar manner but 1 or 2 weeks later. The epidermis of the lower hypocotyl is only lightly cutinized in the loop stage, and tanniferous and resinous materials are beginning to accumulate in the epidermal cells (Fig. 4). Plastids are numerous in the cortical parenchyma cells, pericycle and endodermis. The pericycle cells at this time are almost as long as the cortical parenchyma cells. The endodermis is rather difficult to identify because Casparian thickenings are only lightly developed, and the cells resemble the cortical cells in size and plastid content. Also the endodermis is not always a distinctly defined layer and the Casparian thickenings shift from one layer to another as the endodermis is traced around the hypocotyl. Both the sclereid primordia in the cortex and the greatly elongated elements in the outer phloem region are characterized by enlarged nuclei, the absence of plastids, and the accumulation of what appears to be finely divided tannin particles. The elongated vascular elements continue downward into the radicle, but the sclereid primordia extend downward only to the indefinite region of separation between the lower hypocotyl and upper radicle. The root meristem appears to be incapable of differentiating sclereid primordia and sclereids are lacking in the cortex of the primary root.

The cells of the pericycle elongate as much as the cortical parenchyma cells during approximately the first week of growth. The pericycle cells then undergo a series of transverse divisions and become considerably shorter than the cortical cells. These divisions continue at a reduced rate for 4 or 5 weeks or until the sclereids are mature. Starch begins to accumulate in the pericycle during the first or second week but not in the cortex. The plastids remain as distinct entities in the cortical parenchyma cells but become more dispersed because of continued cell enlargement; they soon disintegrate in the cells of the endodermis.

The sclereid primordia are difficult to identify with certainty in cross section until 10 to 15 primary xylem cells have matured (Figs. 5 and 6). The cell walls are slightly thickened but still plastic. Most of the idioblasts do not show intrusive growth but all portions of the walls elongate and maintain contact with adjacent cells. If an intercellular space forms near the end of an idioblast, the enlarging cell may push into this space and develop the pointed end characteristic of intrusive growth. This is unusual, however, and most of the mature sclereids have blunt ends. If the idioblast is in firm contact with cells at both ends and intercellular spaces appear along the sides of the cell, the idioblast may become sinuous and distorted because it is elongating at a faster rate than adjacent cells. This also indicates that elongation of these cells is associated with growth of the entire cell wall.

The primary phloem is clearly differentiated at this time and the enlarged outer elements, designated as "precursory elements" by Chaveaud (1902 a, b) are easily distinguished from the smaller, inner phloem elements (Fig. 5). The "precursory elements" have been considered as part of the primary phloem by Allen (1947 b), Gunckel and Wetmore (1946), Spurr (1950) and others. Chaveaud (1902 b) also considered these elements as sieve cells, and in his description of the primary phloem of *Thuja* indicated that the outer "precursory elements" had small sieve areas on the inner walls while the inner elements had them on all walls. This is also true for the phloem in the seedlings of Douglas-fir. The sieve areas are not distinct in embryos or seedlings less than a week old.

The vascular cambium becomes continuous in the lower hypocotyl when the seedling is approximately two to three weeks old (Fig. 9). The outer primary phloem elements are gradually crushed by the formation of secondary phloem. The cells of the endodermis are clearly differentiated and usually show degenerating nuclei and few plastids but no starch. The epidermal cells are more heavily cutinized and contain abundant tanniferous and resinous substances as do the outer cortical parenchyma cells. The cell walls of the sclereids are appreciably thickened but still immature.

By the time the vascular cambium has produced 4 to 6 cells in each tier of secondary xylem, usually at about 6 weeks, the hypocotyl shows more marked changes in structure. The epidermal cells have a heavily cutinized outer wall, a fairly heavy cuticle, and are packed with tanniferous and resinous materials (Fig. 10). The outer 2 to 4 layers of cortical parenchyma cells have thickened cellulose walls and many cells have also accumulated large amounts of resinous compounds. Some of the inner cortical cells begin to collapse and the outer intact cells contain few plastids and very little starch. The endodermal cells are empty and Casparian strips that are relatively thin cover most of the radial and transverse walls. Some of the endodermal cells collapse. The sclereids are essentially mature (Figs. 7, 8 and 10) but most still contain a nucleus, a thin sheath of cytoplasm and tannin granules. Resins or mucilage rarely appear in these cells. The sclereids have narrow, obliquely slanted pits that broaden toward the inner layers of the lignified secondary walls. Some transverse divisions are still occurring in the pericycle which now contains considerable amounts of starch. The primary phloem has mostly collapsed by this time and is crushed between the pericycle and secondary phloem.

There are indications that seedlings from the two sources used differ with regard to the number of sclereids produced. On the basis of relatively few seedlings, those from the Snoqualmie National Forest averaged 39 sclereids in cross sections of the lower hypocotyl, and those from the Mt. Hood National Forest averaged 47 sclereids. However, a study of large numbers of seedlings might give different results.

A cork cambium originates by periclinal divisions in the outer cells of the pericycle (Fig. 11). Usually this occurs during the sixth or seventh week, or when there are 7 to 10 cells in each tier of secondary xylem. This cork cambium is a continuation of the one that originates slightly earlier in the pericycle of the radicle. Shortly after the first periclinal division both daughter cells accumulate large amounts of finely granular material which stains heavily with safranin. Usually the outer cells of this division become the cork cambium. The endodermis and most of the inner cortical cells are collapsed but the outer cortical cells with thicker walls and resinous substances remain turgid. The pericycle cells contain numerous starch grains and a few accumulate resinous substances. The cork cambium in the epicotyl does not develop until 2 to 4 weeks later when it originates in the subepidermal cells of the cortex and the cortex remains green even though several cell layers of cork are produced this first year.

When the first cork cells are produced, the anthocyanins disappear and the hypocotyl begins to turn brown. Both periclinal and anticlinal divisions are frequent as the cambium continues to form cork to the outside but usually no parenchyma to the inside. The cortex is quickly killed (Fig. 12) and is soon split longitudinally by continued increase in diameter of the hypocotyl. Fungal hyphae have been observed in the remnants of the dead cortex but apparently they cannot readily penetrate the cork layer. The heavy accumulation of tanniferous and resinous materials that stain with safranin (Figs. 12 and 13) seems to be characteristic of the cork cambium of Douglas-fir since the radicle and also in older stems (Grillos, such deposits occur in the cork cambium of

1956). As cork is matured in the hypocotyl, the granular material which is responsible for the staining reaction disappears and droplets of yellowish, unstained resin remain. Some woody cork is produced which is derived from phellum and does not represent transformed phelloderm as suggested by Chang (1954) for the bark of older stems.

The development of other tissues of the hypocotyl is typical. The pericycle and phloem parenchyma cells proliferate slowly as the hypocotyl increases in diameter with the addition of secondary vascular tissues. The early secondary phloem elements collapse toward the end of the growing season. Many of the parenchyma cells in both pericycle and secondary phloem accumulate resinous materials. The outer cells of the pericycle develop somewhat thicker walls and resemble collenchyma cells. Few remnants of the cortex are present when growth ceases and the hypocotyl is protected primarily by several layers of cork cells (Fig. 13).

Secretory Cells

In addition to the anatomical changes discussed, the use of the term "secretory cell" as applied to Douglas-fir should be clarified. This term has been applied to elongate subdermal cells and to outer phloem cells in many conifer embryos and seedlings. These cells in Douglas-fir, though similar in method of origin and structure in the embryo, differentiate into greatly different types of elements.

"Secretory cells" associated with the primary phloem of Douglas-fir have been described from the embryo and radicle and hypocotyl of the young seedling (Allen, 1947 a, b), from the roots, hypocotyl and cotyledons (Messeri, 1935), and from young shoots of older trees (Sterling, 1946, 1947 b). The same distribution also occurs in other conifers. These cells in the embryo originate from the outer portion of the procambium following either transverse or longitudinal cell divisions. In pine (Spurr, 1950) they more frequently follow longitudinal division. In the embryo most of the vascular "secretory cells" are easily recognizable because they differentiate early and become greatly elongated by the intercalary growth of the embryo. In the seedling, however, the new "secretory cells" produced by the intercalary meristem below the cotyledonary node are usually shorter when mature and resemble more closely the outer elements of the "precursory phloem." As the hypocotyl develops, the distinction between "secretory cells" and outer phloem elements becomes less and less. Most of them develop tapered ends instead of the square ends usually seen in the embryo. While sieve areas have not been observed in the walls of the longest elements of this type, the nuclei degenerate and the cells collapse in much the same manner as the outer elongate cells of the "precursory elements," now considered to be the outer phloem elements by most investigators. The evidence suggests that the elongated elements in the outer phloem of the embryo, usually termed "secretory cells," should be considered as the first elements of the primary phloem that reach such lengths only because of their early differentiation.

The elongate "secretory cells" scattered throughout the cortex of the hypocotyl in both embryo and seedling are clearly sclereid primordia. These differentiate following transverse divisions in the developing embryo and also in the intercalary meristem in the upper hypocotyl of the seedling. Chaveaud (1904) mentioned briefly that in the leaf of *Abies*, but not in the stem, the "secretory cells" became transformed into fibers. This type of sclereid primordium is confined to the hypocotyl and cotyledons of Douglas-fir and does not occur in the cortex of the radicle or epicotyl. Thus these primordia result only from intercalary growth and not from apical meristems. Elongation is by longitudinal expansion of the radial and tangential walls while adjacent cells are under-

going division and elongation. The primordia which are differentiated early in the development of a given region result in much longer sclereids than those differentiated late.

Eight other species of conifers were checked for sclereids by cutting free-hand sections of the hypocotyl of seedlings 5 to 6 weeks old. Sclereids were found in all species but the number and distribution in the cortex varied with different genera. In *Chamaecyparis lawsoniana* (A. Murr.) Parl. and *Libocedrus decurrens* Torr. the the sclereids were limited to the first layer of cells underneath the epidermis. In *Abies grandis* (Dougl.) Lindl. and *A. procera* Rehd., the sclereids occurred almost entirely in the inner layer of the cortex next to the endodermis, but in *A. concolor* (Gord. & Glend.) Lindl. and *A. magnifica* var. *shastensis* Lemm., sclereids were located in the inner three or four layers of the cortex. Sclereids were rare or lacking in *Pinus ponderosa* Laws. and *P. pinaster* Ait. Since elongated cells similar to the sclereid initials of Douglas-fir occur in the embryo of *Pinus strobus* L. (Spurr, 1950), additional investigation to determine the fate of these cells is indicated.

The sclereids in the hypocotyl differ in origin and method of growth from sclereids in other parts of Douglas-fir. Sclereids originate in the pith and cortex of young shoots on older plants by irregular growth of parenchyma cells into intercellular spaces (Sterling, 1947 a). These sclereids are very irregular in shape with many long arms extending in various directions. The sclerenchyma cells in the secondary phloem of older trees are usually referred to as "phloem fibers" (Chang, 1954) or "bast fibers" (Kiefer and Kurth, 1953). These are not phloem fibers, i.e., fibers derived directly from fusiform cambium initials, but are sclereids. Shimakura (1936) recognized these as "fibrous sclerotic cells" but did not indicate their origin. These sclereids are derived from secondary phloem parenchyma cells that start enlarging in phloem that is approximately one year old (Grillos, 1956). They develop mostly in a longitudinal direction by intrusive growth and usually have tapered ends and extremely thick walls.

Discussion

Various investigators have shown that young seedlings of Douglas-fir are the most sensitive to heat injury, and that resistance increases with age. The extensive anatomical changes during development of the hypocotyl undoubtedly affect the ability of the seedling to resist injury by heat but the degree of protection provided by the various structural changes cannot be estimated at the present time. Possibly any structure that would tend to insulate against high soil temperatures and reduce the amount of irradiation that penetrates the deeper tissues would protect in some degree. On this basis the young seedling, until shortly after the loop stage, is protected only by a very thin cuticle and the slightly thickened outer walls of the epidermal cells. During the next few weeks the cuticle and outer walls became progressively thicker, and tanniferous and resinous compounds accumulate in the epidermal and outer cortical parenchyma cells. The walls of the latter cells become thicker, numerous intercellular spaces appear in the inner cortex, and the sclereids develop heavy secondary walls. The endodermal cells develop Casparian thickenings and the cell contents gradually disappear. By the fifth to seventh week, the vascular cambium has produced several cells in each tier of secondary xylem and phloem. Resinous materials continue to accumulate in the outer cortical cells and starch in the pericycle. Some of the inner cortical parenchyma cells collapse. Baker (1929) suggested that this collapse might be due to the development of the endodermis. This undoubtedly plays a part since at this time the endodermal walls are suberized, have lost all cell contents and have started to collapse. However, increase of secondary tissues and lack of cell division

in the cortex must also be involved in this initial collapse of cortical cells.

The cork cambium originates usually within 6 to 8 weeks by periclinal divisions of the outer cells of the pericycle, and is followed by the browning and shrinkage of the cortex. As additional cork and secondary vascular tissues are produced, the cortex collapses completely, splits longitudinally, and is mostly sloughed late in the growing season. By the end of the first season of growth, the vascular cambium, which is very sensitive to heat, is protected by a few remnants of the dead cortex, the cork layer, thickened walls of the outer cells of the pericycle, accumulations of tanniferous and resinous materials in the cork cambium, pericycle and phloem parenchyma cells, and finally by the collapsed primary and early secondary phloem.

Summary

The anatomical development of the hypocotyl from the mature embryo through the first season of growth is described. The cork cambium, which is probably the most important single development that would affect heat resistance, originates in the pericycle when the seedling is 6 to 8 weeks old. The cortex is soon killed by cork formation and is sloughed by the end of the growing season.

The elongated "secretory cells" described for conifer embryos are of two distinct types in Douglas-fir. The elongated cells distributed throughout the cortex of the hypocotyl are sclereid primordia and, with similar cells produced by an intercalary meristem in the upper hypocotyl, mature into sclereids in 5 or 6 weeks. The vascular "secretory cells" appear to be phloem elements that become unusually long because of early differentiation together with the intercalary growth of the hypocotyl.

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Influence of the Forest Tent Caterpillar Upon the Aspen Forests of Minnesota

BY
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SEVERE DEFOLIATION by the forest tent caterpillar, *Malacosoma disstria* Hbn., (Fig. 1) has occurred in northern Minnesota at about 10-year intervals since the earliest records reported for the late 1870's. The 1933-38 outbreak was the most extensive and the longest of any reported up to that time. In many localities quaking aspen, *Populus tremuloides* Michx., was defoliated for as many as three consecutive years.

FIGURE 1. *Forest tent caterpillars congregated in a dark mass on the trunk of a quaking aspen.*

At the beginning of the current outbreak in 1948, heavy defoliation was reported first from localities near Leech Lake and along the shores of Basswood Lake. The

The authors are Associate Professor, School of Forestry, and Professor, Department of Entomology and Economic Zoology, respectively, University of Minnesota. They wish to acknowledge assistance without which this study could not have been completed. A. E. Schneider did much of the initial planning and worked closely with the project in its first year. The field work was done by Ronald Froelich, Harold Batzer and Daniel Meyer who also analyzed data and prepared progress reports. Cherng-jiann Shiue assisted materially with the statistical analysis and several useful techniques were suggested by R. I. Beazley. Both R. M. Brown and S. R. Gevorkiantz were helpful in connection with the mensurational aspects of the problem; the former also reviewed the manuscript. The study was made possible through a cooperative grant from the office of Iron Range Resources and Rehabilitation Commission, the assistance of the State Entomologist, and all of Minnesota's major forestry agencies.

Published as Sci. Jour. Ser. Paper No. 3740 of the Minnesota Agricultural Experiment Station.

accompanying maps (Fig. 2) show the rate and extent of development of the outbreak through 1956. This outbreak has been much more extensive and severe than any of the previous ones, aspen having been defoliated for two to three consecutive years over very large areas. In the spring of 1957, the caterpillar population had been reduced to a low level by natural control agents over most of the area infested during the past few years, but some heavy defoliation can be expected at least through 1957. Thus the current outbreak will have lasted at least four years longer than the one that persisted from 1933 to 1938.

From scattered records following the 1933-38 outbreak, estimates of tree mortality varied from none to as high as 80 percent. A mortality of about 20 percent of the severely defoliated trees was mentioned quite commonly. This outbreak coincided with the mid-thirties drought which may have accentuated the damage.

The present study relating to the impact of the forest tent caterpillar upon the timber resource was undertaken because of the

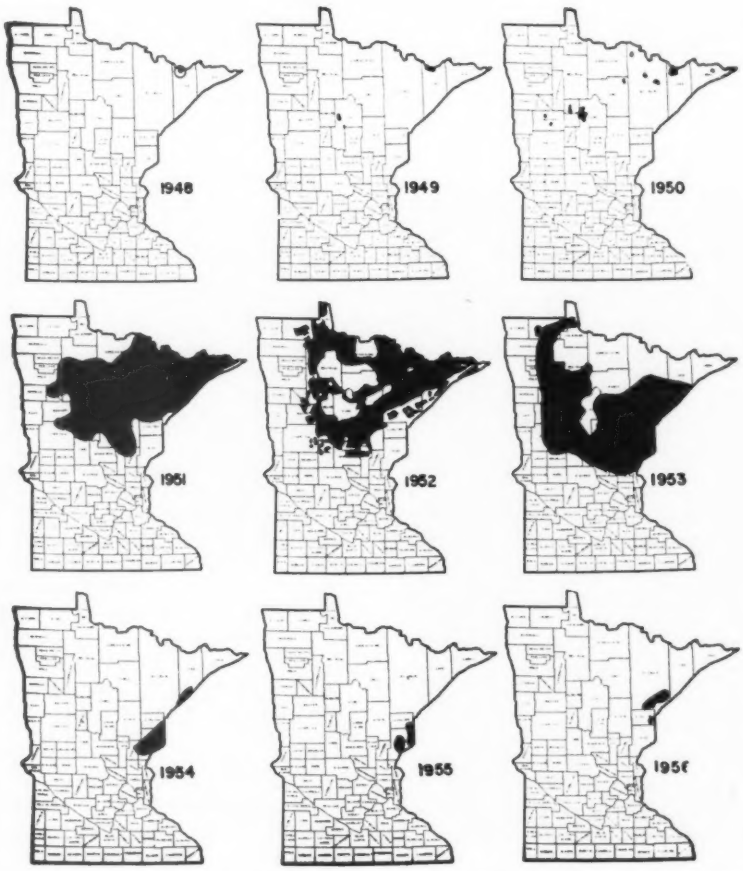

FIGURE 2. *Distribution of the forest tent caterpillar outbreak in Minnesota, 1948-1956.*

increasing significance of aspen in Minnesota's forest economy. The over–all objective has been to determine the effect of defoliation by the forest tent caterpillar upon the management of aspen stands in northern Minnesota. Questions having direct bearing on this objective include:

1. How much if any, aspen mortality may be attributed to defoliation?
2. Does defoliation reduce aspen growth? If so, how much reduction occurs?
3. How quickly does aspen growth recover following cessation of defoliation?
4. Does defoliation indirectly encourage other causes of aspen loss such as poplar borers or Hypoxylon cankers?
5. What is the influence of defoliation upon the growth of conifers in the understory?
6. What is the effect of the caterpillar upon the brush species of the forest?

In 1953, a research project supported by funds of the Iron Range Resources and Rehabilitation Commission, was initiated in an attempt to answer these questions. It was conducted jointly by the School of Forestry and the Department of Entomology and Economic Zoology of the University of Minnesota.

Establishment of Study Areas and Field Methods

Areas of known defoliation histories were selected for study from information available in the files of the Department of Entomology at the University and from the State Entomologist. Supplementary information on defoliation was obtained from State forest supervisors and rangers. Circular sample plots were then established on these areas, having their centers at least two chains inside the type in which they were established. These were placed at convenient locations along roadsides over a wide area in the northern part of the State. Since they were not randomly selected, all statistical analyses are limited by this consideration. At the time that the plots were initially chosen, an effort was made to have a variety of defoliation histories represented.

The plot size was selected after determination of tree diameter. Where average d.b.h. was 2.5 inches or less, plot size was 1/50 acre; where it was 2.6 inches to 4.5 inches, plot size was 1/20 acre; and where it was 4.6 inches or larger a 1/10 acre plot was established.

Ninety seven plots were established in 1953, 39 of which were diagrammed for future studies involving individual trees. The 97 areas were revisited during the summer and fall of 1954 and at that time, trees on 28 additional plots were numbered. One new plot, having a mean diameter of less than 2.5 inches, was also established since only a few of the 1953 plots contained aspen of small sizes. By 1955, 80 plots suitable for study remained (Fig. 3); the others were destroyed or omitted for one reason or another.

FIGURE 3. *Location of study plots in northern Minnesota.*

The information recorded on each aspen plot can be divided into three parts: (1) general plot information applying to the type as a whole; (2) individual tree data; and (3) measurements for calculating growth of the stand. In addition, the coniferous understory was observed on many areas. These areas may be subdivided into those carrying pole-sized balsam fir and those with smaller trees (advanced regeneration).

General Plot Information

Site index of the stand was determined from two dominant aspen trees. Age was determined by adding two years to the number of annual rings counted from cores extracted from the trees at breast height. Height was measured with an Abney level and crown closure was estimated to the nearest 10 percent.

Estimates of defoliation intensity prior to the initiation of the study were based on the following criteria:

Complete: All broadleaved trees and brush completely stripped of leaves, except red maple which is not fed upon by the caterpillar. No cocoons in trees.

Heavy: Aspen trees completely stripped and conspicuous feeding damage on other species including birch and brush.

Moderate: Occasional aspen completely stripped, most aspen with tops thin; little feeding on birch or brush.

Light: No trees showing complete defoliation. Feeding damage confined to top of aspen crowns. Little or no feeding on other tree or brush species.

None: No leaves removed from crown of any tree species. Terminal branches with normal foliage.

Defoliation histories before field work began were derived from observations by personnel of the state and federal forest services. Intensity of current aspen defoliation was observed in each year of the study and classified as above.

In 1953, the quantity of brush cover was estimated and recorded in one of the following classes:

Light—less than 1/3 of the ground area shaded.

Medium—1/3 to 2/3 of the ground area shaded.

Heavy—more than 2/3 of the ground area shaded.

Species were listed in descending order of abundance. The preference of brush for feeding by forest tent caterpillar larvae was estimated and species were listed in descending order of preference.

The intensity of 1953 brush defoliation was designated by the following categories:

Complete: All brush species completely defoliated.

Heavy: Nearly all brush completely defoliated; feeding on all remaining leaves.

Moderate: Few brush stems completely defoliated with conspicuous feeding on most remaining leaves.

Light: Only occasional conspicuous feeding on brush leaves.

None: No evident forest tent caterpillar feeding on any brush species.

Individual Aspen Tree Data

The following information was recorded for individual trees on all aspen plots in each of the three years of the study:

1. Agencies responsible for mortality were estimated in the event that dead trees or trees with twig dieback were found on plots. Mortality that could not be attributed to disease, mechanical damage or borers was considered a possible result of defoliation. It was thought that unexplained mortality from many plots if correlated with defoliation intensity and frequency would be good evidence relating mortality to defoliation.

2. Crown vigor (Gevorkiantz, *et al.*, 1943) for each tree was classified as follows: head dominants, strong dominants, conditional dominants and codominants, weak dominants and codominants, intermediates or suppressed. These crown vigor classes were assigned a number 1 through 6, respectively.

3. Leaves were classified as being normal or subnormal in size.

4. Wounds, disease, insect attack, and mechanical injury were recorded for each tree.

5. The amount and apparent cause of twig dieback in the crown of each tree was estimated as a percent of the total crown.

6. The intensity of current defoliation was classified as:

Heavy: Leaves completely stripped; or if refoliated, smaller and lighter in color than normal (Fig. 4).

Moderate: Top of crown severely thinned by feeding; no evident refoliation.

Light: Conspicuous feeding damage at top of crown.

None: No feeding on any part of the crown.

In each year of the study, increment cores were extracted at the completion of the growing season from the five dominant, healthy aspens nearest the plot center. Cores were extracted at breast height along the average radius and perpendicular to the bole. Trees bored one year were not rebored in subsequent years.

Coniferous Understory

The following restrictions were placed on trees to be included in the sampling of the coniferous understory:

1. Trees growing within two chains of the edge of the aspen stand were not measured.
2. Only vigorous trees with healthy crowns and apparently good growth were measured, diseased or injured trees being excluded from the sample.
3. No data were collected in grazed or partially logged stands.

Pole-size balsam fir areas. Thirty-seven areas containing pole-size balsam fir (2.5 inches d.b.h. or larger) under aspen were located in 1954 (Fig. 5). These areas were variable in size, depending on the stocking density of the understory, but were large enough to permit observations on five balsams.

FIGURE 4. *Aspen defoliated by the forest tent caterpillar, June, 1937. The non-defoliated trees are red maples upon which the caterpillars seldom feed.*

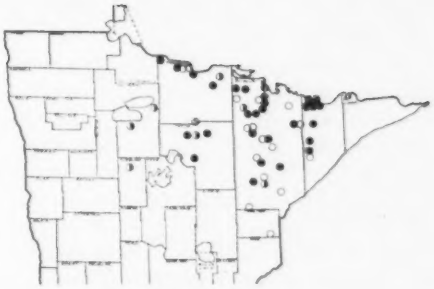

FIGURE 5. *Location of aspen stands containing understories of advanced regeneration and pole-size balsam fir.*

The following data were collected on each of these 37 areas:

1. Five increment cores were extracted at breast height from pole-sized balsam firs. Trees were arbitrarily selected for boring because of the limited number available in each area.
2. Diameters of bored trees were measured to the nearest tenth of an inch.
3. The proportion of the crown of each balsam shaded by the aspen overstory was designated as being one-fourth, one-half, three-fourths or complete. This classification was intended to estimate the degree of competition afforded by the overstory.
4. An increment core was extracted at breast height from each of five dominant aspens on each area. The qualified aspen nearest each bored balsam fir was selected.

Advanced balsam fir regeneration areas. Twenty-four areas containing advanced balsam fir regeneration (0.6 to 2.4 inches d.b.h.) under aspen were located in 1954 (Fig. 5) and studied further in 1955. The sizes of these areas also varied with the density of stocking, but were sufficiently large to permit the measurement of 20 balsams when they were available. Six of

the areas were found to contain less than 20 trees, however.

A mechanical system was devised for selecting trees in the sample. Tree number one was arbitrarily selected well inside the aspen stand. Tree number two was selected on the basis of its being a balsam of suitable size closest to tree number one, etc. In the event that a tree fell within two chains of the stand border, it was ignored and the next closest unmeasured tree was selected.

Since overstory brush may suppress the annual height growth of balsam, only trees which in 1947 were above the level of the brush were measured.

The data collected for each area are listed below:

1. The annual height growth for each of the years 1947 through 1954 inclusive for each balsam was measured with a tape and recorded to the nearest hundredth foot.
2. Annual height growth for the same years was also taken where possible, for each of 20 balsams growing nearby in open areas or under species not defoliated by the caterpillar.
3. One overstory aspen crown closure measurement was obtained for each fir with an instrument called a "moosehorn" (Garrison, 1949). The moosehorn was systematically located on a tripod on the south side of each fir and was leveled with a hand level before readings were taken.
4. At the end of the 1955 growing season, 10 balsam trees were bored on each plot studied that year, and increment cores extracted for the study of growth.
5. Increment cores were also extracted from five dominant aspens in the overstory in 1955. These were used to compare growth responses with those found in balsam and as a basis for verifying defoliation histories.

Effect of Defoliation Upon Aspen

Size of Leaves

An obvious effect of the heavier intensities of defoliation upon aspens is reduced average leaf size and a tip-clustering tendency on the part of leaves which are produced the year after defoliation. Leaf size was determined by ocular examination in 1953, 1954 and 1955. Data available in 1955 permitted analysis using the two defoliation histories supplying the greatest number of plots. These include one year light defoliation and two years heavy defoliation. The percentage of trees with normal leaf development was computed for each plot. After transforming these percentages into angles, (Snedecor 1946) two split-plot analyses of variance were used, one comparing the first year following defoliation with the second (22 plots), the other comparing the second year with the third (14 plots).

The first analysis showed a highly significant difference between the percentage of trees with normal leaf size one year following defoliation and the corresponding percentage two years following defoliation. Only 9 to 12 percent of all trees were estimated to have normal leaf development one year following the last previous defoliation while between 63 and 88 percent of all trees had normal leaf development two years after defoliation. No significant differences in the percentage of normal sized leaves were found in either of the two years among the three defoliation histories.

Fourteen different plots with suitable histories were similarly analyzed the second and third year after defoliation. From 95 to 98 percent of the trees had normal leaves the third year. No significant differences existed in leaf size associated with defoliation histories or with the years since defoliation occurred.

Twig Dieback

Dead twigs in the upper portions of aspen crowns, first observed in 1953, were estimated and recorded for individual trees in the two succeeding years. It was assumed that heavy twig dieback in the crown, if it occurred, might be the result of defoliation and might indicate declining vigor eventually leading to mortality. In an effort to see if this were true, the volume of twig dieback was estimated as a percent of the total crown. Where this dieback could not be attributed to whipping by the crowns of

adjacent trees, and occurred on otherwise healthy trees, it was assigned to defoliation.

If defoliation were the cause, twig dieback would be expected to increase with the heavier intensities or frequencies of defoliation. Eighty plots composed largely of aspen and having known defoliation histories were used for the analysis. The number of trees having twig dieback on each aspen plot was related to intensity of defoliation in 1951, 1952, and 1953.

Since only relationship was desired, a correlation was used assuming linearity within the limits of the data. A highly significant positive partial correlation was found between the number of trees exhibiting twig dieback in 1954 and the intensity of defoliation in 1953. Heavier intensities of defoliation in 1951 and 1952 may have contributed to the total number of trees with twig dieback in 1954 but their contributions were not significant.

On the basis of these findings, one might expect the number of trees per plot with dieback in 1953 to be dependent on the intensity of defoliation occurring in 1952. In that year, more plots underwent heavier intensities of defoliation than in 1953. If one assumes that only defoliation of the previous year is directly related to the amount of dieback it would be expected that more trees should have shown twig dieback in 1953 than in 1954. Although 1,117 trees had twig dieback in 1954 only 135 trees showed twig dieback in 1953. This inconsistency can be explained by the possibility that defoliation intensity plus other factors, or combinations of factors, were responsible for dieback.

Is dieback an indication of declining vigor leading to subsequent aspen mortality? The 66 plots on which individual tree records were available for 1954 and 1955 were used in the analyses.

In order to determine the nature and extent of dieback attributable to the tent caterpillar, the number of healthy trees with no twig dieback was computed for each plot and totaled for 1954 and 1955. Similarly, trees having 20 or more, 10 to 19, 5 to 9, less than 5, and 0 percent twig dieback were recorded and totaled (Table 1). In each year trees having twig dieback represent about one-third of the total number of trees. Of more importance, less than 3 percent of the total number of trees exhibited 10 percent or more dieback in either year. On the basis of these data, there appears to be no increase in total number of trees with dieback between 1954 and 1955.

A study made in 1954 to determine whether development of twig dieback on 230 individual trees had increased or decreased between 1953 and 1954 showed that 4 trees (less than 2 percent) had increased in crown dieback more than 20 percent. All four were of suppressed crown classes. A similar study made in 1955 revealed the same pattern. All otherwise healthy trees on the 66 plots which exhibited some twig dieback in 1954, in 1955,

TABLE 1. Number of trees classified by per cent of dieback in 1954 and 1955.

Percent of crown with twig dieback	1954		1955	
	Number of trees	Percent of total	Number of trees	Percent of total
0	2051	71.3	1747	63.5
1 to 4	635	22.1	869	31.6
5 to 9	122	4.2	75	2.7
10 to 19	46	1.6	19	.7
20 to 99	24	.8	40	1.5
Total	2878	100.0	2750[1]	100.0

[1]128 trees free of other insect, disease, or mechanical injury died between 1954 and 1955 (see Tables 7 and 8).

or in both of these years were tabulated on the basis of increase, decrease, or no change in the amount of twig dieback (Table 2). A Chi-square test shows that recovery is dependent upon the original degree of dieback. Those trees having heavy original dieback show larger proportions with increased dieback than those having lighter original dieback. The difference in total number of trees in Table 1 and Table 2 is explained by trees which had no twig dieback in either year.

It is apparent that there has been no marked increase in twig dieback and that only a very small proportion of the trees have increased more than 20 percent between these two years. Of the 25 trees showing more than a 20 percent increase in twig dieback, 22 were of suppressed crown classes. The large amount of dieback evidenced by these trees appears to be largely the result of suppression rather than of caterpillar defoliation.

Stem Growth

Defoliation Effects. To ascertain the probable influence of defoliation upon aspen growth, an evaluation of the effects of various frequencies and intensities of defoliation was made and the results were compared with growth during the years immediately preceding defoliation. In these comparisons it has been assumed that growth during defoliation years, except for the effects of defoliation, would have equaled that in years preceding defoliation. Should climatic conditions, such as rainfall, vary substantially in these two periods, growth loss evaluations by this method would not be accurate. The problem of precipitation difference, however, is considered in a later section.

An analysis was made in 1953 of increment cores extracted at breast height from 5 dominant, apparently healthy aspens on each of the 97 study plots established that year. This permitted comparison of radial growth under a particular intensity of defoliation with the average radial growth of the same trees during a three-year period (1947-1949) preceding defoliation. These data (Batzer, *et al.*, 1954) indicate that radial growth was reduced with increasing intensity and frequency of defoliation. Growth during the third year of heavy defoliation was essentially similar to that of the second successive year of heavy defoliation.

In subsequent studies, basal area growth was used in preference to radial growth because it is a better estimate of volume growth. The accuracy of basal area comparisons as a measure of the influence of defoliation upon volume growth is predicated upon these assumptions:

1. That basal area growth at breast height is a good index of the volume growth of the tree.
2. That growth changes similar to those found on the bored dominants also occur among the weaker crown classes. This is of minor importance since most of the potentially merchantable volume is distributed over

TABLE 2. Number of trees increasing, decreasing and remaining the same in amount of twig dieback between 1954 and 1955.

1954 Percent of crown with twig dieback	1955 Number of trees showing			
	Increase	Decrease	No change	Total
1 to 4	393	278	406	1077
5 to 9	22	48	19	89
10 to 19	13	10	6	29
20 to 99	25	0	4	29
Total	453	336	435	1224

TABLE 3. Analysis of variance for the basal area growth of aspen during different defoliation histories, 1954 data.

Source of Variation	Degrees of freedom	Mean Square	F	F'	5% level F	1% level F
Histories	4	14.0091		15.90**	4.12	7.85
Site	1	0.2418		1.62	6.59	16.69
Age	1	2.0533		3.50	7.71	21.20
History × Site	4	0.2617	1.28		2.46	3.51
History × Age	4	0.6319	3.10*		2.46	3.51
Site × Age	1	0.0128	15.91		253.00	6334.00
Error	104					

*Significant at the 5% level.
**Significant at the 1% level.

the dominant trees.

3. That growth during years immediately preceding defoliation is a reliable indicator of the amount of growth that would have occurred had there been no defoliation.

Basal area comparisons in 1954 were based on 10 cores per plot, 5 of which had been obtained in 1953. The remaining 5 were obtained on the same plots but from different healthy, dominant trees than those bored in 1953. From the measurements made on each core, basal area growth was computed by the formula

$BA_g = \pi G(D+G)$

where:

BA_g equals basal area growth in square inches

G equals width of a growth ring in inches

D equals diameter of the tree inside of each growth ring.

Plots were classified into 5 defoliation classes (none, first year light, first year heavy, 1 year heavy following 1 year light, and the second year heavy), 2 site classes (index 49-68 and index 69-87) and 2 age classes (20-34 years and 35-49 years). The average basal area growth for each was then compared. Highly significant differences occurred in annual basal area growth in stands having different defoliation histories (Table 3). When age classes were compared, highly significant differences occurred only in years of no defoliation, whereas with defoliation, there was so great a reduction in growth in all age classes that no significant differences appeared. No significant differences were found between average basal area growth in the two site classes as defined by site index.

The average basal area growth of aspen in square inches using 1954 data were: without defoliation, 1.923; during the first year of light defoliation, 1.617 (84%); during the first year of heavy defoliation, 0.547 (28%); during the year of heavy following light defoliation, 0.400 (21%); and during the second year of heavy defoliation, 0.258 (13%). Tukey's honestly significant differences for these data were computed to be 0.361 at the five per cent level and 0.434 at the one per cent level of significance. For these data then, growth during the first year of light defoliation is not significantly different from that during no defoliation but that during the first year of heavy is very significantly different from that during light. During heavy defoliation after a year of light, growth is not significantly different from either that during the first year of heavy defoliation or that during the second year of heavy defoliation, nor is growth during the second year of heavy significantly different from that during the first year of heavy defoliation.

In analyzing 1955 data, each year of defoliated growth on each plot was paired with the average growth occurring in the

five years immediately preceding defoliation on the same plot. The effects of site and tree age on defoliated growth were not considered in this analysis, making possible the inclusion of data from a maximum number of plots.

Average annual basal area growth was computed for each plot from five increment cores extracted in 1955. Growth during years of defoliation on each plot was paired with the average growth occurring in the five years preceding defoliation. Growth data were also classified by defoliation histories and t tests were used to determine whether any differences existed between the average growths in the various history classes. The histories compared were first year light, first year of heavy, second year of heavy, 1 year of light immediately following 1 year of heavy and 1 year of light following 2 successive years of heavy defoliation. The significant results of these tests are summarized below. The analysis of all other possible defoliation history combinations showed no significant effects (Table 4).

1. Highly significant differences exist between growth during first year light defoliation and growth during all other histories.
2. Highly significant differences exist between light defoliation immediately following a year of heavy and growth during the second year of heavy defoliation.
3. Highly significant differences occur between one and two successive years of heavy defoliation.
4. A significant difference occurs between light defoliation immediately following two successive years of heavy defoliation and the second year of heavy defoliation.

Additional t tests indicated that the plots with these histories did not differ significantly in years prior to defoliation.

In addition, it was necessary to determine whether growth during each history was significantly different from the average growth occurring immediately preceding defoliation. Highly significant differences occurred between average growth in the five year period preceding defoliation and growth occurring within each defoliation history except first year light. Growth during first year light defoliation was not significantly different from that occurring in the preceding five years. Suddarth (1954) has proposed a method by which the magnitude of the differences existing between two populations can be predicted, with desired probability, from samples taken from the two populations. An analysis of the data by his method shows with 95 percent confidence, that on these plots average growth was reduced to

TABLE 4. Comparisons of basal area growth following various defoliation histories using data from increment cores taken in 1955.

History 1		History 2					
Defoliation	Basal area growth in sq. ins.	Defoliation	Basal area growth in sq. ins.	Degrees of Freedom	t	5% level t	1% level t
Heavy, 1 yr.	.392	Heavy, 2 yrs.	.193	72	5.38**	1.994	2.648
Heavy, 1 yr.	.392	Lt. after 2 H.	.359	59	.43	2.000	2.660
Lt. after 2 H.	.359	Heavy, 2 yrs.	.193	29	2.21*	2.045	2.756
First yr. Lt.	1.308	Lt. after 1 H.	.582	58	5.26**	2.000	2.660
Lt. after 1 H.	.582	Heavy, 1 yr.	.392	70	1.81	1.994	2.648
Lt. after 1 H.	.582	Lt. after 2 H.	.359	27	1.81	2.052	2.771
Lt. after 1 H.	.582	Heavy, 2 yrs.	.193	40	3.78**	2.021	2.704
First yr. Lt.	1.308	None	1.238		n.s.		

*Significant at the 5% level.
**Significant at the 1% level.

35 percent of normal during light defoliation immediately following a year of heavy, to 28 percent during the first year of heavy defoliation, to 17 percent during light defoliation which immediately follows two years of heavy, and to 13 percent of normal during the second year of heavy defoliation. The reductions in growth very closely approximate those found in the 1954 analysis.

Rainfall Effects. The quantitative evaluations of growth losses during defoliation, as presented in the preceding section, are qualified by the assumption that without defoliation, average basal area growth would have come from a population of means which is not different from the average computed for the five years preceding defoliation. The calculated growth losses are representative only in the event that the effects on growth of factors other than defoliation were similar in both periods.

A major climatic variable influencing aspen growth is precipitation. Therefore, a study was undertaken to ascertain the influence of April, May, June, and July precipitation upon the basal area growth of aspen, both in years preceding defoliation and in years during defoliation. Average annual basal area growth for each of 77 study areas (Fig. 6) was computed from those increment core measurements of the 5 dominant aspens used in evaluating growth losses. Annual growth was then related to the April to July rainfall occurring at the closest weather station (Fig. 6). The years preceding defoliation include those from 1940 to the first year of the recent caterpillar outbreak. Although this outbreak began as early as 1949 on some areas, on others it did not begin until as late as 1953. Since the defoliation period, including all levels of defoliation, has varied in length from 1 to 5 years, both the number of years preceding defoliation and those during defoliation vary for the several study areas.

In the analysis, the effects on growth of rainfall, site class, tree age, and relative

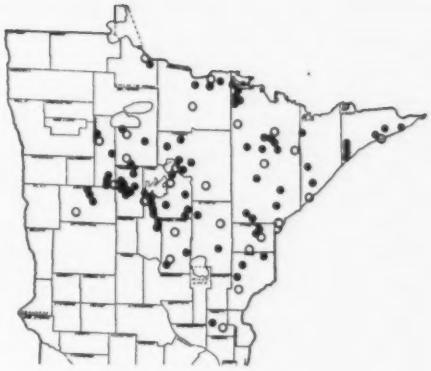

FIGURE 6. *Location of aspen stands and weather stations used in rainfall study.*

stand density (actual basal area expressed as a percentage of that found in normal yield tables for similar stands) were separated by analysis of variance (Table 5). Site class (as defined by site index) and relative stand densities were based on stand measurements which had been made on each study area in 1953 corroborated by further study in 1955.

As shown in Figure 7, basal area growth increases, though not proportionately, with rainfall increases during April to July in years prior to defoliation. A better understanding of the major variables (rainfall, site index, relative stand density, and age) can be obtained by partitioning the degrees of freedom of each variable into linear and curvilinear components as described by Goulden (1952, Chap. 10). A highly significant curvilinear regression is found between rainfall and aspen growth in years preceding defoliation. This is a positive slope indicating that as rainfall increases, growth increases, though at a decreasing rate. Highly significant curvilinear regressions were also found between basal area growth and relative stand density, site in-

TABLE 5. Analysis of variance showing relationships among four sources of variation affecting the basal area growth of aspen, separated into linear and curvilinear components.

Source of variation	Degrees of Freedom	Mean Squares	F	5% level F	1% level F
Rainfall classes	4	28.925	16.77**	2.38	3.35
Linear	1	80.430	46.63**	3.85	6.68
Curvilinear	3	11.757	6.82**	2.61	3.81
Site classes	4	29.887	17.33**	2.38	3.35
Linear	1	69.950	40.55**	3.85	6.68
Curvilinear	3	16.533	9.58**	2.61	3.81
Relative density classes	4	41.248	23.91**	2.38	3.35
Linear	1	122.900	71.25**	3.85	6.68
Curvilinear	3	14.030	8.13**	2.61	3.81
Age classes	6	108.570	62.94**	2.11	2.83
Linear	1	527.440	305.76**	3.85	6.68
Curvilinear	5	24.796	14.37**	2.22	3.05
Error	829				
Total	847				

**Significant at the 1% level.

dex and tree age (Table 5). Thus, basal area growth per tree is larger on better sites and in older stands. Growth, on the other hand, decreases with increasing relative stand densities.

No significant correlations were found between basal area growth and rainfall in years of defoliation, even though the precipitation range was about the same as in non-defoliation years (Fig. 8). Basal area

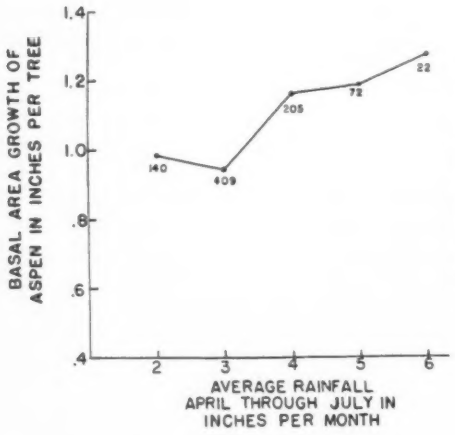

FIGURE 7. *Average basal area growth of aspen in non-defoliation years as related to average monthly precipitation April through July.*

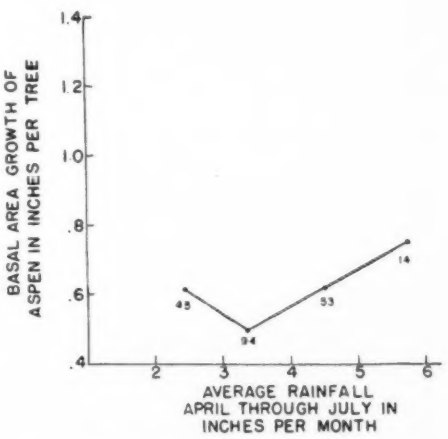

FIGURE 8. *Average basal area growth of aspen during years of defoliation as related to average monthly precipitation, April through July.*

growth for the non-defoliation period may be seen in Figure 7 to range from 0.94 to 1.28 square inches, with an average of 1.03 per tree. This variation is correlated with an average monthly precipitation range during April to July of from 2 to 6 inches. Although a similar range of precipitation occurred in defoliation years, basal area growth per tree ranges from 0.50 to 0.74 with an average of 0.57 square inches. During the second year of heavy defoliation, average basal area growth is still further reduced to an average of 0.26 square inches per tree. The much greater influence of defoliation as compared with precipitation is apparent.

These findings lead to the rejection of the hypothesis that lower rainfall has been the dominant contributing factor in the growth reduction which has accompanied forest tent caterpillar defoliation. They serve to strengthen the original hypothesis that a large proportion of the serious basal area growth reductions, viz., 72 percent in the first year of heavy defoliation, and 87 percent in the second year of heavy defoliation, is the direct result of caterpillar feeding.

Growth Recovery Following Cessation of Defoliation

In order to determine the rate of normal growth recovery for aspen following years of defoliation, basal area growth on each plot in years following defoliation was paired with the average growth occurring in the five years preceding defoliation. The paired data were classified by the number of years since a particular intensity and frequency of defoliation.

Comparison of growth the first year following cessation of defoliation with growth during the five years preceding defoliation using t tests gave these results (Table 6):

1. A highly significant difference existed between growth during the first year after one year of heavy defoliation compared with growth in the period of no defoliation.
2. A highly significant difference occurred between growth during the first year after two years of heavy defoliation and growth in the period of no defoliation.
3. Significantly less growth occurred between the first year after light following two successive years of heavy defoliation and growth in a period of no defoliation.
4. No significant difference was found between the growth occurring during the year after a light defoliation year following one year of heavy defoliation compared with growth during the period of no defoliation.

Growth losses the first year following cessation of defoliation using Suddarth's θ value at the 95 percent confidence level showed that on the plots measured, a reduction of 22 percent still occurred 1 year after 1 year of heavy defoliation, of 16 percent during the first year after 2 years of heavy defoliation, and of 16 percent 1 year after light defoliation which followed 2 successive years of heavy defoliation. No significant differences in growth occurred among

TABLE 6. Comparison of basal area growth one year following the last year of defoliation with that occurring during the five years preceding defoliation.

Defoliation history	Degrees of freedom	t	5% level t	1% level t
Heavy, 1 yr.	6	3.89**	2.447	3.707
Lt. after 1 H.	16	1.47	2.120	2.921
Heavy, 2 yrs.	5	5.70**	2.571	4.032
Lt. after 2 H.	8	2.45*	2.306	3.355

*Significant at the 5% level.
**Significant at the 1% level.

these three histories both in years of defoliation and in years preceding defoliation.

Growth in the second year following defoliation was not significantly different from average growth during a five-year period of no defoliation. In other words, aspen showed nearly complete recovery in the second year following the last defoliation as well as a nearly complete recovery one year after the last defoliation where the last year was light.

Tree Mortality

It is difficult to ascertain the agent, or group of agents, which actually caused death by examining the dead tree. However, if death from known agencies is eliminated and the residual mortality is significantly related to intensity of defoliation, there is evidence (but not proof) for assuming defoliation to be the cause. Even without such a relationship, however, it is still possible that defoliation is a contributing factor in mortality caused, primarily or in part, by other agents. No direct evidence on this point was obtained.

In 1953, the year following the first defoliation on several of the plots, all trees which had recently died on the 97 study areas were noted with their probable cause of death. No aspen mortality on any of the 97 areas could be attributed solely to defoliation by the forest tent caterpillar. Since tree records prior to 1953 were not available, on many of the plots it was necessary to estimate the time of death from certain characteristics such as the fineness of twigs adhering to the branches, condition of the bark and presence of dead leaves on the trees.

In 1955, the 37 plots which had individual tree records for two years were used in a study to determine the nature and extent of tree mortality on these areas since 1953. In addition, 29 other plots having individual tree records only between 1954 and 1955 were similarly studied. In an effort to determine whether any mortality was caused by defoliation, the dead trees were tallied on the basis of their crown class and probable cause of death. Dead trees exhibiting mechnical injuries, *Fomes* or *Nectria* cankers, or evidence of poplar borer, were tallied under these respective headings since it would be difficult to determine what part defoliation played in their death. Trees having more than one of the above possible causes of death were tallied by the most probable cause. For instance, a dead tree having both *Fomes* and *Hypoxylon* would be tallied under *Hypoxylon* as the most probable cause of mortality. In the case of wind breakage where the tree had been previously weakened by *Saperda* or some mechanical injury, it was tallied under the agency which had weakened the standing tree. Wind was considered the cause of death only where there was no visible evidence of previous injury or decay at the point of breakage, or when the tree was uprooted. Trees which had died and had none of the previously mentioned characteristics were placed in an "unknown" category.

Table 7 presents the results of the tally of dead trees on the 37 plots containing two years of tree records. A preponderance of dead trees are in the *Hypoxylon* and unknown categories. Over 95 percent of this latter category is composed of suppressed trees. The 29 additional plots for which only 1954 and 1955 records were available were analyzed and the data are summarized in Table 8. The pattern is similar to that of the 37 plots presented in Table 7. *Hypoxylon* and unknown causes account for nearly all the mortality. As in Table 7, over 90 percent of the unknown category is in the suppressed crown class.

The high percent of suppressed trees in the unknown categories indicates that suppression may be the cause of death. This is a reasonable assumption since some natural mortality of low vigor trees is expected. Furthermore, trees dying as a result of their unfavorable position in the canopy would not display obvious afflictions other than a dead crown. Although it might be expected that defoliation by the tent caterpillar would hasten the death of suppressed trees

TABLE 7. Number of trees dying on 37 plots between 1953 and 1955 classified by crown class and probable cause of death.

Crown class	Number of live trees at start	Unknown	*Hypoxylon*	Wind	Mechanical injury	*Nectria*	*Saperda*	*Fomes*
Trees dying between 1953 and 1954:								
Dominant	564	1	2	3	1			
Codominant	413	1	6	2	1	2	1	
Intermediate	404	4	6	3		1		
Suppressed	1149	109	24	5	7	1		3
Total	2530	115	38	13	9	4	1	3
Trees dying between 1954 and 1955:								
Dominant	536		5					
Codominant	431		5	2			3	
Intermediate	402	1	4	1		2		
Suppressed	978	76	18	1	7			1
Total	2347	77	32	4	7	2	3	1

this would be difficult to prove. However, an analysis of variance using 1954 data showed no significant relationship between the number of suppressed trees dying between 1953 and 1954 and previous intensities of defoliation.

Barter and Cameron (1955), working in New Brunswick, attribute mortality of aspen to tent caterpillar defoliation since average mortality in the three years immediately following the caterpillar attacks was more than twice as great as in the fourth year. These data are not comparable to the Minnesota data since the stand was 60 years old (approximately 20 years older than the oldest Minnesota stand studied), the trees are not classified according to crown class, and but one stand was sampled. In Minnesota, since 1953 there have been only 4 of a total of 396 trees which died where death cannot be explained by known causes, or reasoned to be the result of a suppressed crown condition. Therefore, there is no evidence in these data that defoliation alone caused aspen mortality.

Occurrence of Poplar Borers

Defoliators have been reported by several authors to reduce the vigor of trees to the extent that they become more susceptible to attacks by other insects, particularly borers (Craighead, 1950; Felt and Bromley, 1944; *et al.*). In order to determine

TABLE 8. Number of trees dying on 29 plots between 1954 and 1955 classified by crown class and probable cause of death.

Crown class	Number of live trees at start	Unknown	*Hypoxylon*	Wind	Mechanical injury	*Nectria*	*Saperda*	*Fomes*
Dominant	429	2	8	1		1		
Codominant	308		4	1			2	
Intermediate	263	2	3				2	
Suppressed	501	40	15	1	1	1	1	2
Total	1501	44	30	3	1	2	5	2

TABLE 9. Percentage of plots attacked by Saperda calcarata *classed by number of trees infested and related to defoliation histories.*

No. infested trees per plot	Less than one year heavy		One year heavy		Between one year and two years heavy[1]		Two years heavy		More than two years heavy	
	1954	1955	1954	1955	1954	1955	1954	1955	1954	1955
1 or more trees	25	25	19	35	23	23	29	53	42	50
3 or more trees	8	0	0	12	0	0	12	24	25	33
5 or more trees	0	0	0	8	0	0	6	18	17	25
Total plots	12		26		13		17		12	

[1]For example, 1 year light and 1 year heavy or 1 year moderate and 1 year heavy.

whether populations of the poplar borer, *Saperda calcarata,* are related to defoliation by the forest tent caterpillar, observations were recorded for individual trees both in 1954 and 1955. Although the lack of observations for years prior to 1954 has made this problem difficult to evaluate, should the occurrence of borers be greater on the more severely defoliated plots, then it would appear that defoliation does contribute to borer abundance.

On the 80 plots for which the occurrence of various insects had been recorded for individual trees both in 1954 and in 1955, 33 plots had some *Saperda* damage in either or both of these 2 years. When these data are classified by defoliation histories, the plots with the higher occurrence, both in total numbers and in percentages (Table 9) of infested trees per plot, appear to have undergone the heavier intensities and frequencies of defoliation. For example, 8 of 12 plots which contained 3 or more infested trees in either 1954 or 1955 had undergone at least 2 years of heavy defoliation. More striking results are obtained when plots with 5 or more infested trees in either of these 2 years are considered. Six of 8 plots with 5 or more infested trees had previously undergone at least 2 years of heavy defoliation. The remaining 2 plots had undergone only 1 year of heavy defoliation. One plot was on a very poor site and of relatively older age (45 years). That the high infestation on this one plot may be a normal condition is supported by Graham (1952), who reports that slow growing trees are most susceptible to attack by poplar borers.

Although heavier intensities of defoliation may have increased the incidence of *Saperda* in some stands, it can be concluded that on these plots poplar borer infestations have not become serious following the recent outbreak of the forest tent caterpillar.

Occurrence of Hypoxylon cankers

It is difficult to deaermine if the occurrence of *Hypoxylon* has increased as a result of defoliation. However, if an increased percentage of trees killed by *Hypoxylon* is shown to be related to frequency and intensity of defoliation, it might be reasonable to assume that defoliation by the tent caterpillar has resulted in a higher mortality from this disease.

The percentage of trees killed by *Hypoxylon* just prior to 1953 was computed for the 39 plots established in 1953. Similarly, the percentage of trees killed by *Hypoxylon* on 37 of these plots between 1953 and 1954, and between 1954 and 1955 was computed (Table 10). There is no significant difference in the percentage of trees killed in any of the three years. On 29 areas, established in 1954, the percentage of trees killed by *Hypoxylon* just prior to 1954 was computed, together with the percentage killed between 1954 and 1955 (Table 10).

There are no significant differences between the percent of trees killed by *Hypoxylon* on the 29 plots in the years studied. Furthermore, no significant differences were found to exist between the percent of

TABLE 10. Trees killed by Hypoxylon *by years.*

Year	No. living trees	Trees killed No.	Percent
Thirty-seven plot test:			
Just prior to 1953	2735	41	1.5
Between 1953 and 1954	2530	38	1.5
Between 1954 and 1955	2347	32	1.4
Twenty-nine plot test:			
Just prior to 1954	1576	35	2.2
Between 1954 and 1955	1501	30	2.0

trees dying of *Hypoxylon* on the 37 plots and those dying on the 29 plots in the years studied.

Since there has been no significant increase in the percent of trees killed between 1952 and 1957 on the plots studied, and since the great majority of these plots were severely defoliated at some time during this period, it is concluded that defoliation by the tent caterpillar has not increased the amount of aspen mortality caused by *Hypoxylon*. Whether or not the incidence of *Hypoxylon* has increased is not known.

Effect of Aspen Defoliation Upon the Growth of Associated Balsam Fir

Although defoliation by the forest tent caterpillar significantly reduces the growth rate of aspen, it is reasonable to assume that such losses might be offset to some degree by increased growth of the understory conifers. Preliminary investigations in 1953 indicated that both height growth and radial growth of understory balsam fir might be greater during years of defoliation than in years prior to the caterpillar outbreak.

Radial Growth

To determine the effect of overstory defoliation on understory conifer growth, studies were undertaken in 1954 and 1955 on two different size classes of balsam fir, pole-size (2.5 inches d.b.h. and larger) and advanced regeneration (0.6 to 2.4 inches d.b.h.).

The average annual radial growth of both aspen and balsam fir for the 37 areas with pole-size balsams was computed, when possible, from 5 aspen and 5 balsam cores measured to the nearest .0025 inch. For some areas, the averages were based on 3 or 4 rather than 5 cores (Table 11). These exceptions are accounted for by core breakage or, in some aspens, by wetwood. No average was based on less than three cores, however. All radial growth averages for both species on the advanced balsam regeneration areas were based on five cores for aspen and ten cores for balsam fir.

Neither checks nor precise defoliation records were available for this study. A correlation analysis was first made between the average annual radial growth of aspen and the corresponding growth of pole-size balsam fir. The five years preceding defo-

TABLE 11. Frequency distribution table of growth averages classed by numbers of cores used to calculate average.

Species	Years	Number of Annual Growth Averages Classed by Numbers of Cores in the Average 5 cores	4 cores	3 cores	Total Number of Averages
Balsam fir (pole-size)	1945-49	139	30	14	183[1]
	1950-54	163	17	5	185
Quaking aspen	1945-49	153	30		183
	1950-54	155	30		185

[1]The annual growth for 1945 and 1946 was not computed on one plot because growth measurements were available from only two increment cores.

liation (1945-1949) were included in one analysis. Another analysis related growth of these species on the same areas in years which included forest tent caterpillar defoliation (1951-1954). A correlation analysis was also made between aspen and balsam radial growth in years of defoliation on areas containing advanced balsam regeneration.

The results of these analyses indicate: (1) that in years preceding defoliation, a positive though not significant (5 per cent level) correlation was found between aspen and balsam radial growth on areas with pole-size balsams; (2) that in years during defoliation, a highly significant (1 per cent level) negative correlation was found between aspen and balsam fir radial growth on areas with pole-size balsam as well as on areas with advanced regeneration (Fig. 9). In other words, during years of no defoliation as aspen growth increases, balsam fir growth generally increases and as aspen growth decreases, balsam growth generally decreases although the two are not significantly correlated. During years of defoliation, however, as aspen growth decreases, balsam fir growth for both pole-size trees and advanced regeneration shows a highly significant increase.

This conclusion that the radial growth of balsam fir is increased during periods of defoliation can be further strengthened by classifying the stands according to defoliation histories (Fig. 10). The year or years that heavy defoliation occurs in each area containing understory balsams can be estimated with good reliability on the basis of known defoliation histories on nearby aspen areas. These estimates can be substantiated by noting the years during which aspen growth on the balsam study areas is reduced. The curves presented in Figure 10, although based on different numbers of plots, show consistent increases in balsam growth during the year or years that aspen is heavily defoliated. The fact that these increases occur during different years largely reduces the probability that a climatic factor is responsible.

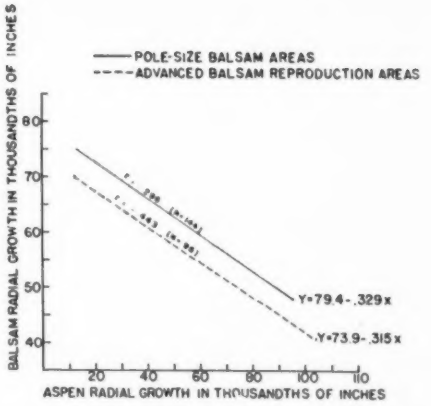

FIGURE 9. *Relationships between the radial growth of aspen and that of balsam fir during years of defoliation.*

Height Growth

In order to determine whether the height growth of balsam fir increases in years during which overstory aspens are defoliated, annual height growth measurements of balsams growing under aspen were obtained. Although no undefoliated aspen stands with balsam understories were available to serve as checks, it was assumed that balsams growing in nearby open areas or under some non-defoliated species like pine, would serve adequately as checks. If the height growth trends of understory balsam firs are similar to those on check areas in years prior to defoliation, any real response in height growth during defoliation should become apparent by inspection of the growth trends. The relative height growth of balsams under aspens and check balsams were compared for the years 1947-1954. Since check balsams could not always be found, these comparisons were possible for only 12 different areas. On all 12 the height growth trends of understory and open grown balsam were found to be very similar both in years prior to defoliation and in years during defoliation (Fig. 11).

Thus it is concluded that there is no obvious height growth response by balsam fir resulting from aspen defoliation.

Defoliation of the Brush Species

Feeding Preference

During the first year of the study, attention was directed to forest tent caterpillar food preferences among brush (shrub) species on 50 plots in which brush feeding was evident. Brush species were listed in descending order of abundance and feeding preference on the basis of visual estimation. Feeding preference estimates were complicated by the fact that in some areas there had been complete stripping of leaves on some brush species and refoliation had taken place by the time the estimates were made. In these situations the otherwise simple listing of brush species in descending order by the amount of leaf chewing noted had to be supplemented by an estimate of cocoon abundance. If about 90 cocoons were collected per 3 minute walking collection and if no cocoons were found on the leaves of the species in question, it was assumed that the larval population had been sufficiently large to completely defoliate that species.

A feeding preference index was calculated for each brush species by multiplying the number of times the species was found to be preferred first, second, third, etc., by a weighting factor. The weighting factor ranged from 1 to 6, 1 denoting first preference, 2 second preference, etc. The sum of these products was then divided by the number of times the species was found to be fed upon. The feeding preference index can be expressed by the formula:

$$p = \frac{(p_1 \times 1 + p_2 \times 2 + p_3 \times 3, \text{etc.})}{N}$$

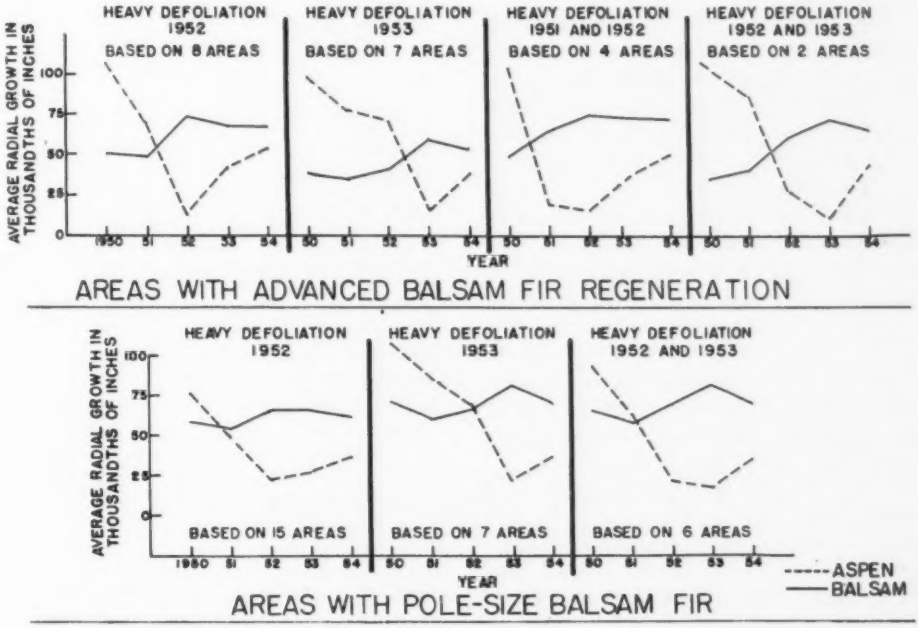

FIGURE 10. *Relationship between aspen and balsam radial growth during different years of heavy defoliation for two size classes of balsams.*

where: p = feeding preference index.
p_1 = number of times species was preferred first.
p_2 = number of times species was preferred second.
p_3 = number of times species was preferred third, etc.
N = total number of times species was fed upon.

The smaller the index value, the greater was the preference for feeding on the species.

The brush species for which the greatest feeding preference was shown were hazel (*Corylus* spp.), followed by prickly ash (*Xanthoxylum americanum*), cherry (*Prunus* spp.), serviceberry (*Amelanchier* spp.), pussy willow (*Salix humilis*), racemose dogwood (*Cornus racemosa*), downy arrowwood (*Viburnum rafinesquianum*), round-leaved dogwood (*Cornus rugosa*), green alder (*Alnus crispa*), and high-bush cranberry (*Viburnum trilobum*) in that order. Wild rose (*Rosa blanda*), mountain maple (*Acer spicatum*), and red osier (*Cornus stolonifera*) were among the least preferred, while moosewood (*Viburnum alnifolium*), honeysuckle (*Lonicera* spp.), raspberry (*Rubus* spp.), and gooseberry (*Ribes* spp.) were not found to be host species.

The feeding preference index (Table 12) is useful in estimating the relative preference of larvae for utilizing brush leaves as food. For example, cherry with an index value of 2.16, serviceberry with a value of 2.36 and pussy-willow with a value of 2.74, lie somewhere between second and third choice. Similarly hazel with an index value of 1.08 is not always the most preferred species but is in rare instances second to cherry or serviceberry. Hazel was observed to be first in feeding preference 43 times, while it was found to be in second place 4 times. All of the brush species listed in Table 12 will rarely be found in a single aspen stand. However, all species observed are listed in descending order of preference.

To show the relative preference for

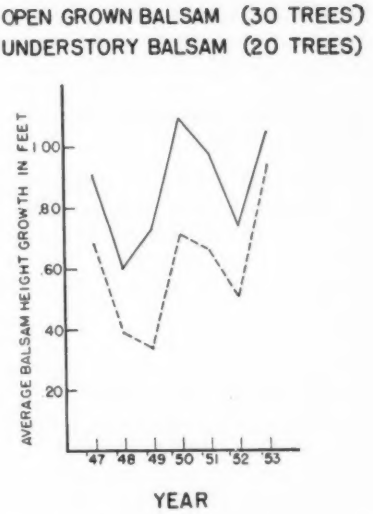

FIGURE 11. *The relationship between the height growth of open-grown and of understory balsam fir as represented by study plot 105. The probable year of heavy defoliation for this plot was 1952.*

TABLE 12. Feeding preference of forest tent caterpillar larvae for leaves of brush species.

Species	Feeding Preference Index
Corylus spp.	1.08
Xanthoxylum americanum	2.00
Prunus spp.	2.16
Amelanchier spp.	2.36
Salix humilis	2.74
Cornus racemosa	3.14
Viburnum rafinesquianum	3.14
Cornus rugosa	3.25
Alnus crispa	3.33
Viburnum trilobum	4.50
Rosa blanda	4.67
Acer spicatum	4.75
Cornus stolonifera	7.00
Viburnum alnifolium	-----
Lonicera spp.	-----
Rubus spp.	-----
Ribes spp.	-----

brush species when compared with their relative abundance, the frequency of occurrence was graphed over the preference rating for some of the more commonly encountered species. It is conceivable that when an ordinarily preferred species is present in low numbers its abundance may be a factor in feeding preference. It is doubtful that there is a strong attraction for any one brush stem by larvae and therefore selection at a low brush species population may be influenced by chance. It is apparent, however, that under normal circumstances abundance is not directly related to the order of feeding preference.

Stem Mortality and Twig Dieback

In 1954, effort was directed toward ascertaining whether stems of hazel brush die after being defoliated by the forest tent caterpillar. Mortality estimations were made in the vicinity of each of 96 aspen plots. The percentage of dead brush (shrub) stems and the average percent of twig dieback (i.e., dead twigs in the upper portions of the brush crowns) exclusive of the dead stems were estimated on these areas. The data were classified (Table 13) into two groups, the first of which included 30 plots on which brush had previously been heavily defoliated. The second group contained 66 plots with no previous heavy brush defoliation. Since brush mortality is common to both defoliated and non-defoliated areas it can be concluded that although defoliation is a factor, other items such as age of shrubs, overstory crown closure, and edaphic factors, in total may contribute more to mortality than does defoliation.

Summary and Conclusions

The periodic epidemic appearances of the forest tent caterpillar which, in the past, have occurred at about 10 year intervals in Minnesota forests, have been of increasing intensity and duration. It is reasonable to expect that the aspen forests of Minnesota, covering about 6,000,000 acres (Guilkey, *et al.* 1954), will be seriously defoliated by this insect in the future. In addition to the effect of the caterpillar upon recreational values, its effect upon timber values and consequently upon forest management for timber production should be of concern to Minnesota forest managers. With the present significance of aspen as a pulp species throughout the Lake States (Horn, 1956), the problem becomes one of considerable potential economic importance.

Serious defoliation in the most recent outbreak, has not caused aspen mortality nor is there evidence that aspen losses to *Saperda* borers or to *Hypoxylon* cankers have increased materially following attack.

Hazel, the most serious detrimental brush species in Minnesota from the forest manager's viewpoint, is the preferred food of the forest tent caterpillar among understory shrubs. It has not been seriously affected, however, since neither stem mortality nor twig dieback increased very ma-

TABLE 13. Stem mortality and twig dieback occurring on defoliated and non-defoliated hazel brush.

Defoliation history of plots	Total Number of plots	Brush Stem Mortality			Brush twig dieback		
		No. of plots	Per cent of plots	Average per cent dead stems[1]	No. of plots	Per cent of plots	Per cent of twig dieback[1]
Plots having had heavy brush defoliation	30	10	33	4	18	60	7
Plots having had no heavy brush defoliation	66	15	23	7	29	44	9

[1]On affected plots.

terially following heavy defoliation.

Defoliation of aspen and brush undoubtedly increases the amount of light reaching the understory species and decreases the transpirational drain upon soil moisture. It might be presumed that such changes in the environment of non-defoliated conifers beneath aspen would increase their growth. These studies have shown that balsam fir trees in the understory in fact have been favorably affected and have responded to aspen and brush defoliation by increased radial growth. The extremely scattered occurrence of other species of conifers beneath aspen has not permitted a study of their response.

Of the approximately 6,000,000 acres of aspen in Minnesota, about 12 percent carry enough conifers in the understory to be completely converted to a coniferous (10 percent) or coniferous-hardwood (two percent) type by the end of the present rotation. Of the coniferous understory, over 85 percent is spruce-fir type, largely balsam fir. About seven percent carry lesser but important amounts of coniferous understory (Heinselman, 1951). In total, only about 19 percent of the aspen area contains an understory of conifers. The volume and growth rate of this understory is far below that of the associated aspen. Furthermore, the increased radial growth in the predominant understory species, balsam fir, is less than one-third of the decrease in aspen radial growth. These considerations make it apparent that aspen volume losses resulting from reduced growth have far exceeded gains in coniferous growth.

The same ecological changes which contribute to increased radial growth in balsam fir may also affect the regeneration of conifers in the understory. This aspect of the problem was not studied but since the primary understory conifer is an extremely tolerant species, particularly in the seedling stage, reduced competition probably does not have great effect. In those few aspen stands where pine seedlings are found, defoliation may help to establish regeneration. Since neither aspen nor brush mortality has followed defoliation, however, and since the stand again closes following reduced populations of the caterpillar, the favorable effects on pine regeneration are probably short-lived.

In its overall effect upon timber values, the forest tent caterpillar is most significant in reducing the growth of aspen. Basal area losses have been found to vary with defoliation intensity and history from very little in the first year of light defoliation to nearly 90 percent of the prospective basal area growth in the second and third years of heavy defoliation. Growth reduction, in the neighborhood of 15 to 20 percent, carried over into the year following cessation of defoliation in stands where heavy attacks had occurred previously.

In a stand with a history of one year of light and two years of heavy defoliation, the reduction in basal area growth might be expected to be about 70 percent during the first year of heavy, about 90 percent during the second year of heavy and about 15 percent during the year of recovery. Total reduction over such a defoliation period would average about 58 percent per year for the three years following the year of light defoliation. This is a reasonable measure of expected volume losses following such a defoliation history.

For an average aspen stand in Minnesota in which the growth may be calculated by dividing the net annual growth of 1,837,000 cords (Guilkey, *et al.* 1954), by the total acreage, net annual growth would be 0.33 cords per acre. The three-year volume loss in this average stand with one year of light and two years of heavy defoliation would approximate 0.6 cords per acre. For a fully stocked aspen stand on good site where net annual growth might approximate 1.3 cords (Brown, Gevorkiantz, 1934), losses with a similar defoliation history would be in the neighborhood of 2¼ cords per acre.

In evaluating the possibilities of control by aerial spraying in future outbreaks where

commercial aspen is threatened with several defoliations, consideration needs to be given to periodic annual growth of the stands. This, in conjunction with predicted growth losses and an assessment of local stumpage values, would permit the forest manager to determine whether he could afford to spray to control the insect strictly on the basis of timber production. Although present stumpage values for aspen do not permit control by spraying, should such values rise, it may be that the forest manager of selected aspen stands will find spraying feasible during future epidemics of the forest tent caterpillar.

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A Timesaving Slide for Trapping Atmospheric Pollen

Equipment Note by Charles X. Grano, Southern Forest Experiment Station, Forest Service, U. S. Department of Agriculture, New Orleans, Louisiana.

One of the simplest methods of determining the relative amount of forest tree pollen in the atmosphere is to trap the grains on a glass microscope slide coated on one side with a sticky substance, and then to count the number of grains per unit area. Insofar as trapping on a plane surface oriented in one direction suffices for sampling, a slide coated with petroleum jelly, glycerine jelly, or some similar medium is generally used (Sarvas[1]). Because these substances have not proved wholly satisfactory (Hirst[2]), pressure-sensitive tape was tried as a substitute.

Cellophane, vinyl, acetate, and polyester tapes provided by the Minnesota Mining and Manufacturing Company were exposed to highly humid air and their dimensional stability observed. The polyester tape proved best. It is a strong, highly transparent, colorless tape that remains flat and undistorted after prolonged exposure to humid conditions. It is marketed as Scotch Brand Polyester Film Tape #850. The ¾-inch width is ideal for pollen slides.

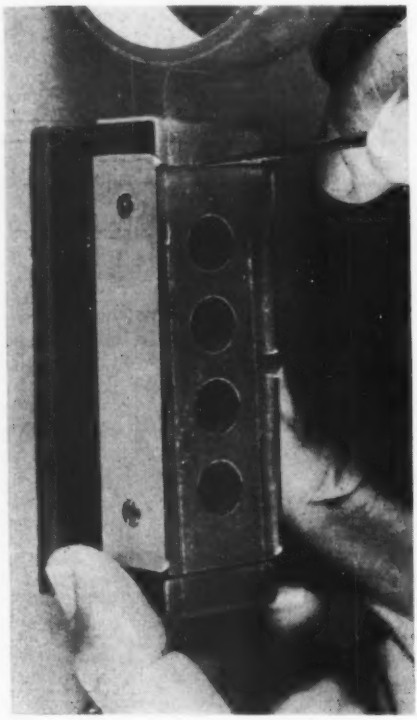

FIGURE 1. *Top view of slide.*

Use of the tape is facilitated by the slide and mounting block (Fig. 1). The slide is made of soft, 30-gage aluminum strip, which is commercially available in rolls 25 feet long and 1⅛ inches wide. The aluminum can be cut easily, with scissors or a paper cutter, to standard microscope-slide dimensions. Four holes or cells measuring 0.4 inch in diameter were made in the slide with an ordinary hand paper punch. Size, number, and placement of the cells may be varied to suit the specific requirements of the user. It is at these perforations that the sticky surface of the tape is exposed and the pollen trapped.

The mounting block is a small piece of 1-inch lumber into which shallow holes were drilled to match those in the slide; these holes prevent marring and contamination of the sticky tape surface exposed in the slide cell. Metal strips secured to the four sides of the block permit easy positioning of the slide over the holes in the block. Putting the tape on a slide requires only a few seconds. To prepare the slide for use, place it on mounting block and affix a strip of tape so that it overlaps both ends of the block. Then cut the tape along each end of the slide, and remove slide from mounting block. When the slide is exposed, the sticky side of the tape should face upward.

After the slide has been exposed and the pollen counted, the tape is easily peeled off. An exposed slide can be made semi-permanent

[1]Sarvas, Risto. 1952. On the flowering of birch and the quality of seed crop. Metsätieteellisen Tutkimuslaitoksen Julkaisuja 40 (7). Helsinki.

[2]Hirst, J. M. 1952. An automatic volumetric spore trap. Ann. Appl. Biol. 39: 257-265.

by taping over its upper surface, so that the pollen is sealed between two layers of tape.

On a microscope with a mechanical stage, the aluminum slide should rest on top of a standard glass slide; otherwise the spring actuated jaws may buckle the soft metal.

Geographic Variation in Pinus contorta

By William B. Critchfield. Maria Moors Cabot Foundation. Publication 3. Harvard University, Cambridge, Massachusetts. 118 pp. (Quarto size).

Review by Jonathan W. Wright
Michigan State University, East Lansing

This book is a revision of Dr. Critchfield's doctoral dissertation submitted to the University of California. The choice of methods, and indeed the choice of subject, strongly reflect the long tradition of outstanding work on experimental systematics at that University and other California institutions. It is a successful synthesis of taxonomic and genetic methods, applied to one of the West's most widespread and variable tree species — lodgepole pine (*Pinus contorta* Dougl.)

The taxonomic portion of the study includes analyses of several leaf and cone characters which were chosen because they were easily studied and subject to relatively little environmental control. The measurements were made on specially collected samples from wild populations in all parts of the species' range and on samples collected from small provenance tests in three different parts of the world. On the basis of these measurements, the species is divided into four moderately distinct subspecies — ssp. *contorta* from coastal Alaska to coastal California, ssp. *bolanderi* from a very limited area of coastal California, ssp. *murrayana* from the Sierra Nevada and Cascade Mountains, and ssp. *latifolia* from the Rocky Mountains and other interior portions of the species range. There was close correspondence between the results of the measurements on the plantation-grown trees and the natural stands.

The genetic portion of the study includes analyses of rate of germination; speed of germination; length, width, and structure of seedling leaves; and duration of seedling growth period. These data were collected from seedlings grown from seed collected in the wild. All characters measured varied with the locality of collection. For example, all samples of ssp. *bolanderi* germinated slowly (average germination time 18 days) and had a long seedling growth period (about 240 days); in contrast, all samples of the Rocky Mountain ssp. *latifolia* germinated rapidly (average germination time 7 days) and had a short (about 100 days) seedling growth period.

Both the taxonomic and genetic portions of the study showed the presence of considerable genetic variation within the subspecies. The within-subspecies variation is not so great as between-subspecies variation, but nevertheless is great enough to justify considerable genetic effort on each of the subspecies. For example, in the coastal ssp. *contorta* there is a north-south cline in duration of the seedling growth period. And in ssp. *murrayana* there is a north-south cline (and probably also an altitudinal cline) in leaf width.

Full and proper use was made of statistics in the genetic portions of this work. But in the taxonomic portion the reader is left to decide for himself the relative strength of the less important tree-environment correlations. The paper could have been shortened considerably—and probably clarified as well—if the word pictures of the doubtfully significant correlations had been replaced by appropriate statements of statistical significance.

Certainly this paper on lodgepole pine is of great theoretical importance to tree breeders and taxonomists. But it is also of immediate practical importance. Lodgepole pine is already a useful exotic in northern Europe, and it promises to be a useful parent of jack-lodgepole hybrids in both eastern and western United States. Just how useful it will be depends upon how quickly we get information on the best provenances. This monograph provides the framework upon which we can plan provenance tests that will give the most results with the least expenditure of effort.

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All figures should be numbered consecutively. If only one is submitted it should be designated Figure 1. On the margin or back of each illustration should be written lightly in soft pencil the number of the figure, the name of the author, and an abbreviated title.

Photographs should be sharp and clear, printed on glossy paper. They should not be smaller than 4 by 5 inches. Sizes 5 by 7 inches and 8 by 10 inches are preferable. Photographs should never be rolled or bent. Care should be taken in fastening photographs with paper clips which often make indentations that show up in reproduction.

Drawings, maps, charts, and graphs are reproduced as line engravings. They should be at least twice as large as they are to appear when reproduced, and should be drawn in india ink on heavy white paper, or tracing cloth.

Footnotes

To indicate a footnote, place a superior figure after the word that refers to the note. Consecutive numerals should be used, never asterisks. Separate the footnote from the text by running a line about one inch inward from the left margin of the type.

Use footnotes to give credit to unpublished material and communications. If only a few references to literature are made (less than one per 1000 words), complete literature citations may be given in footnotes rather than in a separate listing.

Literature Cited

In FOREST SCIENCE practice, references to literature citations are designated by the author's name and year of publication inserted in parentheses at the appropriate place in the text. If there are more than two authors, list only the senior author's name in the text with the abbreviation *et al.* Example: (Smith *et al.*, 1954). Only published references should be given in *Literature Cited*. Periodical abbreviations should follow *Guide to the use of Forestry Abstracts*, Commonwealth Forestry Bureau, Oxford, England, 1950.

Nomenclature and Terminology

When a species is first mentioned in a paper its common name may be immediately followed by its italicized scientific name in parentheses, but this latter name need not be repeated.

As the authority for the exact spelling of tree names, FOREST SCIENCE follows *Check List of Native and Naturalized Trees of the United States (including Alaska)*, Agriculture Handbook 41, Forest Service, U. S. Dept. Agric., Washington, D. C., 1953.

For the spelling of other plant names, contributors should follow *Standardized Plant Names*, 2d Edition, J. Horace McFarland Company, Harrisburg, Pa. 1942.

Technical usage in forestry and allied fields follows *Forestry Terminology*, 2d Edition, Society of American Foresters, Washington 6, D. C. 1950.

There are many style manuals available for the guidance of writers. One of the best is the *Style Manual* of the U. S. Government Printing Office, Washington 25, D. C. 1953.

Webster's *New International Dictionary* is the accepted authority for general spelling.